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ON THE EFFECT OF CRUDE BENZENE HEXACHLORIDE ON CEREAL SEEDLINGS

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There are numerous published references to the unfortunate effects of benzene hexachloride on the development of plants, both from seed (11, 13, 18) and from the tuber (1). In only one of these reports (18), however, is any reference made to the question of the exact identity of the constituent of the crude material which is responsible for these effects. Crude BHC as marketed contains about 70 per cent of the alpha isomer, about 5 per cent of the beta isomer, 12 per cent gamma isomer, some delta isomer, and small amounts of other materials. Of these, the only constituent recognized as important as an insecticide is the gamma isomer. Although from the supposed resemblance in spatial configuration of the molecules of gamma benzene hexachloride and iso-inositol (2, 10, 16) it seemed likely that this isomer was also responsible for the effects on plants, this theory of the activity of gamma BHC now appears to be disproved (3, 20). If the effects on plants were due to some other constituent which could be readily extracted from the crude material, the potentialities of this material for the control of wireworms and other soil insects, both by the preferred method of seed treatment and otherwise, would be greatly enhanced. To settle this question, experiments were begun in March, 1948, by treating seed wheat with various benzene hexachloride preparations and observing the effects on germination and development.

EXPERIMENTS WITH BENZENE HEXACHLORIDE FORMULATIONS

Experiment 1: Uniform percentage of gamma isomer on seed weight

Four batches, each of 25 seeds of Marquis wheat, were treated with the following materials: crude benzene hexachloride containing 10–12 per cent gamma isomer, a dust preparation known as Bennexane 50 containing 6 per cent gamma isomer, and "pure" gamma isomer. The rates of application of each material were such as to give 0.2, 0.4, 0.6, 0.8, and 1.0 per cent of the gamma isomer on the weight of the seed. These dosages were selected on the basis of the work of Thomas and Jameson (19), who obtained 50 per cent mortality of wireworms with applications of 0.28 lb. of gamma isomer to the acre. At normal prairie seeding rates, this would correspond to about 0.5 per cent gamma isomer on the weight of seed. Lower rates than these may well prevent damage or control wireworms (8), for which the rates recommended are from 0.025 to 0.2 per cent; but the adverse effects on plants are roughly proportional to concentration and can best be studied over this dosage range. To ensure retention of the higher dosages of the 12 and 6 per cent materials, a sticker was necessary; the material

selected was Methocel (methyl cellulose) 100 c.p.s., which was applied as a 2 per cent solution to all treated seeds. Check batches of untreated seed, and seed treated with Methocel only were also prepared.

Seed was treated at the end of March, and on April 8, 12 seeds from each of the seventeen batches were planted out in soil, six in each of two 6″ pots, placed for germination in a humidified chamber at room temperature and given abundant water. The remaining seeds from the check batches, and from the highest and lowest dosage rates with each material, were placed for germination on wet filter paper in petri dishes in the dark at 24° C. Observations made on these tests follow in Tables 1 and 2, and Figure 1 shows the appearance of the seeds with the heaviest doses.

Two months after treatment, the remaining treated seeds, which had been stored in the dark, were also set for germination on filter paper. No noticeable differences resulted from the longer storage after treatment.

All batches except the checks showed the symptoms described by other workers in some degree, although these were least pronounced in the seeds treated with pure gamma isomer. Browning and swelling of the root tip, shortness of roots, absence of root hairs, and the short, fat, and flattened coleoptile, were exhibited in some degree throughout. The effects in the coleoptile appear, as Kostoff has stated (11), to be due to changes in the structure of the cells themselves rather than in their distribution and arrangement, epidermal cells appearing as large blisters.

On May 26, 48 days after planting, one series of pot plantings was examined for root growth, and all batches containing living plants from the second series were planted out in open ground. Root growth in the check pots was such that the entire soil content of the pot was closely tied together. In no other pot did the root development approach this, best growth being found from seeds treated with pure gamma isomer at the lowest dosage, in which the roots had just reached the bottom of the pot. Many of the seeds treated at the higher dosages showed no root development at all.

Table 1.—Petri dish germination of wheat seed treated with benzene hexachloride preparations, 12 seeds in each batch. (Experiment 1.)

Treatment	Germination	Root hairs	Av. length coleoptile mm.	Av. length central root mm.
Crude BHC				
0.2% on seed weight	Complete	Nil	2.5	5.0
1.0%	2 failed	Nil	2.0	2.0
Bennexane 50 dust				
0.2% on seed weight	Complete	Nil	2.5	4.5
1.0%	5 failed	Nil	2.0	3.0
Pure gamma isomer				
0.2% on seed weight	Complete	Normal	4.5	15.0
1.0%	Complete	Normal	5.0	10.0
Checks				
Untreated	Complete	Normal	18.0	55.0
Methocel	1 failed	Normal	35.0	95.0

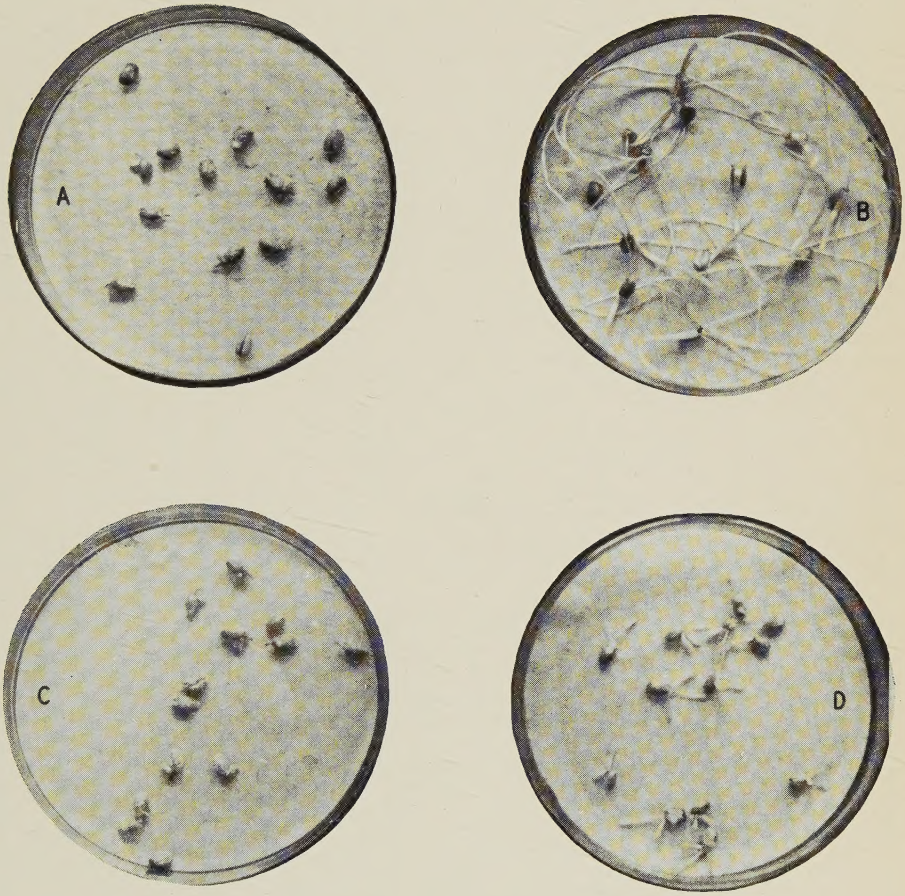

FIGURE 1. Wheat seed germinated after treatment with heavy doses of: A. Crude BHC; B. Check, untreated; C. A dust preparation containing 6 per cent gamma isomer; D. Pure gamma isomer.

TABLE 2.—POT PLANTING OF WHEAT TREATED WITH BENZENE HEXACHLORIDE PREPARATIONS, 12 SEEDS IN EACH TREATMENT, IN TWO BATCHES OF SIX (EXPERIMENT 1)

Material	Per cent gamma on seed weight	Growth in pots			Transferred to open	
		5 days	12 days	48 days	June 21 (75 days)	Aug. 10 (125 days) No. of heads
Crude BHC	0.2	Nil	6 very small	2 normal (4 died)	2 plants heading out	3 very small
	0.4	3 distorted	6 very small	1 normal		
	0.6	1 distorted	2 very small	Nil		
	0.8	Nil	Nil	Nil		
	1.0	Nil	Nil	Nil		
Bennexane 50	0.2	Nil	4 very small	3 normal	3 plants no heads.	4 green
	0.4	Nil	7 very small	Nil		
	0.6	Nil	1 very small	Nil		
	0.8	Nil	3 very small	Nil		
	1.0	Nil	Nil	Nil		
"Pure" gamma isomer	0.2	8 normal	9 normal	9 normal	9 plants heading out	4 very small, 6 small green
	0.4	3 distorted	5 normal, 2 small	5 normal, 1 small	5 plants heading out	4 ripe, 2 green
	0.6	6 distorted	9 normal	7 normal	7 plants heading out	9 small, 3 green
	0.8	2 distorted	4 normal, 3 small	2 normal, 2 small	3 plants heading out	5 small, 7 very small green
	1.0	3 distorted	1 normal, 4 small	2 small	All plants died	
Checks Methocel	Nil	Normal germination and growth			10 plants heading out	9 ripe, 5 green
Untreated	Nil	Normal germination and growth			10 plants heading out	7 ripe, 3 green

Observations were made on the plants transferred to open ground on June 21, and on August 10 when the ears were collected. Seed collected was set for germination 6 months later; early development showed no abnormalities.

Petri dish germination tests were also made using the commercial preparation Benesan E2, a combined mercurial and BHC seed dressing containing 40 per cent gamma isomer, at 0.2 per cent gamma on seed weight, the maximum recommended rate, and at 0.4 per cent.

The lower dosage caused considerable distortion but no reduction in germination; at the higher dosage germination was also affected.

Experiment 2: Uniform percentages of total BHC on seed weight

Batches of 25 seeds of Marquis wheat were treated with the materials used in Experiment 1, to give with each material, the following percentages of total BHC on the seed weight: 0.2, 1.0, 1.8, and 9.0. These percentages are equivalent to the lowest and highest dosages of pure gamma (0.2 and 1.0 per cent) and of crude BHC (1.8 and 9.0 per cent) used in Experiment 1. Fifteen seeds from each batch, and fifteen check seeds, were planted out in the soil on May 26; the remaining seeds were placed for germination on wet filter paper in petri dishes at the same time. In the petri dish germination, seeds treated with pure gamma isomer were slightly in advance at the very early stages, but no other differences between the three materials were observed. Observations were made on plants in the open on June 4 and 21, and on August 10, and are presented in Table 3.

TABLE 3.—GROWTH OF WHEAT SEEDLINGS IN THE OPEN, FROM SEED TREATED WITH BENZENE HEXACHLORIDE PREPARATIONS, 15 SEEDS IN EACH BATCH. (EXPERIMENT 2)

Material	Dosage: % total BHC on seed	Growth on:		
		June 4 (9 days)	June 21 (26 days)	Aug. 10 (76 days) No. of heads
Crude BHC	0.2	Nil	Nil	4 plants, 1 small
	1.0	Nil	2 plants	3 plants
	1.8	Nil	Nil	Nil
	9.0	Nil	Nil	1 small plant
Bennexane 50	0.2	Nil	8 small plants	8 plants, 8 green
	1.0	Nil	3 small plants	1 small plant
	1.8	Nil	Nil	1 small plant
	9.0	Nil	Nil	Nil
Pure gamma isomer	0.2	Nil	2 small plants	2 plants, 2 green
	1.0	1 small plant	Nil	Nil
	1.8	1 small plant	1 small plant	Nil
	9.0	Nil	Nil	Nil
Check (untreated)	Nil	1 normal	7 normal	8 plants, 7 green

EXPERIMENTS WITH CONSTITUENTS AND BREAKDOWN PRODUCTS OF BHC

Experiment 3: Isomers of BHC and a mixture of trichlorobenzenes

This experiment was conducted on the same lines as Experiment 1 except that only petri dish germination tests were used. The materials tested were the alpha and beta isomers, two samples of gamma isomer,

one freshly prepared, melting point 110–112° C., and a second deteriorated, melting point 90–100° C.; and a mixture of trichlorobenzenes prepared from the alpha BHC and consisting of at least 85 per cent of the 1,2,4-isomer. Several authors (6, 12, 16) have shown that BHC breaks down to give, among other substances, trichlorobenzene and hydrochloric acid.

Batches of fifty seeds each of Thatcher wheat were treated with methocel, followed by each of these substances at 0.2, 1.0, and 5.0 per cent on the weight of seed, the trichlorobenzene mixture after emulsification in distilled water with Triton X-100. Germination tests were repeated four times,

TABLE 4.—PETRI DISH GERMINATION OF WHEAT SEED TREATED WITH VARIOUS CONSTITUENTS OF CRUDE BENZENE HEXACHLORIDE. (EXPERIMENT 3.)

Treatment material	Per cent on seed weight	Germination in tests				Total	Remarks
		1	2	3	4		
Alpha BHC	0.2	8/10	10/10	8/10	8/10	34/40	Slight deformity especially at higher dosages in tests 1, 2, and 3. Pronounced deformity in 4.
	1.0	8	8	7	7	30	
	5.0	8	6	9	7	30	
Beta BHC	0.2	6	9	10	7	32	Normal development in all tests.
	1.0	5	10	10	8	33	
	5.0	8	10	10	6	34	
Pure gamma BHC	0.2	7	9	10	7	33	Typical deformation; more severe at heavier dosages, and particularly severe in test 4.
	1.0	8	9	9	6	32	
	5.0	7	8	7	5	27	
Deteriorated gamma BHC	0.2	7	8	9	6	30	Different from pure gamma in degree only; 5% and 1% approx. equivalent to pure gamma at 1% and 0.2% respectively.
	1.0	10	10	6	5	31	
	5.0	8	4	10	5	27	
Trichlorobenzenes	0.2	7	5	5	10	27	Germination somewhat slow, but when it occurred, normal development followed. At higher doses a white pulpy mass surrounded by brown discoloration developed at the normal point of emergence of the radicle.
	1.0	0	0	0	1	1	
	5.0	0	0	0	0	0	
Check	—	9/10	9/10	10/10	10/10	38/40	Normal development.

once immediately after treatment, again after 10 and 20 days' storage in the dark, and finally after a further 10 days' storage exposed to daylight under glass, during which time the seed was exposed to sunlight for about 12 hours. The first two tests were run at a temperature of 24° C., and the last two at day temperatures of 20° C. and night temperatures of 15° C. Ten seeds from each batch were used in each test. The results of these tests are recorded in Table 4. In addition to increased phytotoxic effects after insolation, a pronounced increase in the characteristic musty odour of the alpha and both samples of gamma isomer was noticed.

Experiment 4: Gamma BHC, trichlorobenzenes and HCe in the vapour phase

In Experiment 3 the following materials show distinct physiological activity: pure gamma BHC, deteriorated gamma BHC, and the mixture of trichlorobenzenes. A further experiment was done with these three materials and hydrochloric acid in which the germinating seeds were

TABLE 5.—PETRI DISH GERMINATION OF WHEAT SEED EXPOSED TO THE VAPOUR PHASE OF VARIOUS CONSTITUENTS OF CRUDE BENZENE HEXACHLORIDE. (EXPERIMENT 4.)

	Germination		Remarks
	1	2	
Pure gamma BHC vapour	10	8	Mean root length reduced 30% by comparison with check. This may be regarded as statistically significant, the probability of chance occurrence being less than 0.02. No other obvious symptoms of deformation.
Check	10	10	Normal development.
Deteriorated gamma BHC vapour	10	7	Mean root length reduced 58% by comparison with check, significantly greater than the reduction with pure gamma. Germination slow. No other obvious symptoms of deformation.
Check	10	10	Normal development.
Trichlorobenzenes vapour	0	0	No signs of any development at all.
Check	10	10	Extreme deformation of every seedling, typical of heavy seed treatment with solid gamma BHC.
Trichlorobenzenes vapour in sealed containers	0	0	No signs of any development at all.
Check	10	9	Normal development.
Trichlorobenzenes vapour 24 hr. dose	8	9	Typical gamma BHC seed treatment deformation in every embryo.
Check	10	10	Normal development
Hydrochloric acid vapour	10	9	Normal development.
Check	10	10	Normal development.

exposed only to the vapour phase. Ten seeds were used in each batch, and a separate check batch was used for each material. Watch glasses, each containing a liberal quantity of the appropriate material, were placed in the petri dishes in which the seeds were set for germination. Germination was carried out in the dark at a temperature of 24° C., each test batch accompanied by its check batch, and isolated from the other test batches.

Owing to the surprising results obtained in the check batch of seeds associated with the trichlorobenzene mixture (see Table 5), this experiment was repeated, and the most stringent precautions against contamination of the check batches were taken; the results were identical. Finally, two further repetitions of the trichlorobenzene test alone were made; first, using containers with airtight closures, and second, in petri dishes in which only a very small amount of trichlorobenzene was used, an amount which had completely volatilized within 24 hours.

Experiment 5: The vapour of trichlorobenzene isomers on several varieties of cereals

In this experiment the seeds were germinated on washed sand in large petri dishes. The treatment material was placed in a watchglass at the centre of the dish, and the seeds of the different varieties were separated from each other by radial strips of cardboard, the batches arranged in a random manner around the periphery. Six representative varieties of wheat, (Durum, Rescue, Thatcher, Marquis, Red Bobs and Kharkow) three varieties of oats, (Ajax, Victory and Larain) and three varieties of barley, (Montcalm, Newal and O.A.C. 21) were used. The materials used for the treatment were the 1, 2, 3, and the 1,3,5-isomers of trichlorobenzene, prepared by chlorination of paranitroaniline followed by diazotisation and further chlorination, and presumably free of other isomers, and the material described under Experiment 3, containing at least 85 per cent of the 1,2,4-isomer. A fourth batch with no treatment was run as a check. Germination was at 27° C.

No germination whatsoever occurred in any variety exposed to the vapour of the 1,2,4-isomer. In the vapour of the 1,2,3-isomer, all varieties showed some germination except for the wheats Durum and Kharkow, and the oats Ajax and Victory. After 8 days, however, all plants were dead. It is noteworthy that the only oat variety to germinate was Larain, which also made the best growth in the vapour of the 1,3,5-isomer. In the vapour of the 1,3,5-isomer, all varieties germinated and although growth was very much retarded in comparison with that in the check batches, the plants survived and all were living after 12 days.

Among the wheat exposed to the 1,3,5-isomer, Durum was retarded appreciably more than the other varieties in the early stages, but after 8 days there were no detectable differences. Among the oats, Ajax and Victory were appreciably more retarded than Larain; and among the barleys O.A.C. 21 was most retarded, and Montcalm least.

A sample of pure 1,2,4-isomer proved unobtainable, but confirmatory tests were run with crude material from two other sources: (1) prepared by the chlorination of benzene, and reported to "contain about 95 per cent 1,2,4-trichlorobenzene, most of the impurities consist of isomers of tetrachlorobenzene, with very low percentages of dichlorobenzene isomers", and

(2) "1, 2, 4-trichlorobenzene and 5 to 10 per cent of the 1,2,3-isomer—boiling range in the neighbourhood of 2 to $2\frac{1}{2}$° C. from initial boiling point to dry point; orthodichlorobenzene and paradichlorobenzene are probably not present, and we are fairly certain that the tetrachlors are not present either,—the material contains no free hydrochloric acid." No differences could be detected in the reactions to the original sample and to these two further samples.

In view of the fact that 2,4-dichlorophenol, a component of the 2,4–D molecule, has been mentioned as a breakdown product of benzene hexachloride (14), seeds were also germinated in various concentrations of the vapour of this material. The reactions were closely comparable to those obtained with 1,2,4-trichlorobenzene.

DISCUSSION

The results of Experiment 1 are anomalous; they suggest that the deformation of the seedlings is neither due to the gamma isomer as such, nor yet definitely due to any other major constituent. Analysis and melting point determinations made on the gamma isomer material after these tests indicated that this was very close to 100 per cent gamma isomer. Possible explanations of the greater effect obtained with the preparations of crude benzene hexachloride are: first, that the effect is a non-specific one, due to benzene hexachloride in any form; this is unlikely, in view of the very different physical characteristics and probably spatial arrangement of the molecules, and the similar severity of symptoms obtained with the 50 and 100 per cent preparations. A second possibility is that the effect is due to an impurity operating at very low concentration, perhaps a volatile breakdown product either of several of the isomers, or of the gamma isomer alone. Such a volatile product would be maintained at higher concentration in the proximity of the seed by the heavier coating of other isomers and diluent on seeds treated with preparations of the crude material, which would account for the more severe symptoms with these preparations.

The practical conclusions from Experiment 1 are, first, that if seed treatment with BHC is practicable at all, a refined product with high gamma content is desirable; second, that the margin of safety between a dose which will control wireworms, and a dose which will imperil the plant, at least under difficult moisture conditions, is probably none too great. Although germination and growth of the next generation is not affected, as Kostoff (11) has shown, the integrity of a strain would be threatened by repeated treatments.

Experiment 2 was designed to decide finally if the effect was non-specific and due to BHC in whatever form. The soil germination tests suggest that this is not so, seed treated with pure gamma isomer giving a markedly poorer stand than that treated with preparations of the crude material. The earlier appearance of seedlings from seed treated with pure gamma isomer is peculiar; in the petri dish tests a similar effect was noticed, but no other conclusions could be drawn from these tests. It should be mentioned that while this experiment might be expected to distinguish between a non-specific activity of BHC in any form, and activity of the gamma isomer, if the activity were due to a breakdown product, the ages of the respective samples might be the more important factor.

The results of Experiment 3 also appear somewhat anomalous. The beta isomer may be regarded as physiologically inactive and the alpha isomer almost so; this finally establishes the fact that the effect is not a non-specific activity of BHC. The two samples of gamma isomer each produced what may be regarded as typical "gamma deformation" symptoms, while the mixture of trichlorobenzenes had a pronounced effect on germination, inhibiting this completely at the two higher dosages, and reducing it to about 50 per cent at the lowest dosage. The normal development of the seeds germinating at the lowest dosage of trichlorobenzenes suggests that these are two separate and distinct effects. The distinctly more severe deformation symptoms given by the deteriorated sample, containing a lower proportion of gamma isomer, again suggest however that these symptoms are caused, not by the gamma isomer itself, but by a breakdown product of this. Breakdown, to give this product, appears to be accelerated by exposure to sunlight, which also favours the production of materials responsible for the characteristic odour of crude BHC.

Experiment 4 was designed to test the suggestion advanced in the discussion on Experiment 1, that a volatile breakdown product was the physiologically active material. As so often happens, a fortuitous occurrence in this experiment provided a clue to the solution of the problem as a whole. The consistent deformation obtained in the untreated checks accompanying trichlorobenzene treatments, viewed in the light of the results in sealed containers and with limited dosage, was clearly due to the vapour of the active material diffusing out from under the cover of the treatment petri dish and into the adjacent check petri dish, in sufficient concentration to produce typical "gamma deformation" without affecting germination. This also indicates that the two apparently separate effects described in the previous paragraph are really identical, inhibition of germination being the ultimate form of the symptoms. The results obtained with the two gamma isomer preparations confirm those in Experiment 3.

This demonstration of volatility of the phytotoxic principle also permits an explanation of the absence of deformation at the lowest dosage of trichlorobenzene in Experiment 3; the active material had presumably been dissipated by volatilization before growth had commenced, and in the absence of gamma isomer no more was produced.

Gavaudan and Gavaudan (4) have demonstrated similar deformation of wheat seedlings germinated in air saturated with the vapour of a number of different materials, among them 1,3,5-trichlorobenzene. Experiment 5 was designed to show whether this, or some other material, was mainly responsible for the phytotoxic effects observed with BHC, and at the same time to see whether varietal differences in response to these materials existed.

1,2,4-trichlorobenzene appears to be by far the most important phytotoxic material, although considerable toxic effect is produced by the 1,2,3-isomer and some by the 1,3,5-isomer. It appears likely that the differences are an expression of differences in vapour pressure, and that the molecular toxicities of the three materials are similar. The formation of 2,4-dichlorophenol may be of some significance, and is particularly interesting inasmuch as Meunier (14) describes the odour of the mixture of chlorophenols which he obtained in terms which would apply remarkably well to that of crude

BHC. In normal conditions, a mixture of these phytotoxic materials appears to be produced in most effective proportions and amount from the least stable gamma isomer, in threshold amounts from the alpha isomer, and in quite unimportant amount, if at all, from other isomers. The varietal differences do not appear sufficient to justify plant breeding recommendations, although Durum wheat is possibly peculiarly susceptible, and Larain oats and possibly Montcalm barley are somewhat resistant.

As other workers have observed (9), damage to seedlings tends to be much less in soil germination than in petri dishes. This may be partly attributable to adsorption of toxic materials by soil particles, and partly to better ventilation. It should be noted that poor moisture conditions, when impaired root development is of the greatest importance, are normally associated with good soil ventilation. The work of Smith (17) would seem to suggest that slower breakdown under soil conditions may also be a factor.

The very small amounts in which the 1,2,4-trichlorobenzene is effective, suggest that it might have applications in the field of weed control, possibly if incorporated in place of 2,4-dichlorophenol in a molecule of the 2,4-D type.

Although the literature does not adequately reflect this, BHC has often given anomalous results as an insecticide; some of these results may be explicable on the basis of differences in breakdown reactions under different conditions. Trichlorobenzenes have been shown to have some insecticidal properties themselves (7, 15) and Guilhon (5) has shown crude BHC to be more toxic than its content of gamma isomer would suggest.

SUMMARY

Wheat seed was treated with various preparations and constituents of crude benzene hexachloride, and germinated to decide which of these constituents was responsible for the deformation of the seedlings.

This deformation is not due to the accepted insecticidally active principle, the gamma isomer. A mixture of trichlorobenzenes prepared by the breakdown of alpha BHC possesses this activity in far higher degree, relatively small doses causing the ultimate symptom—inhibition of germination. The material is active in the vapour phase. The most active material in this mixture is 1,2,4-trichlorobenzene, followed by the 1,2,3, and lastly the 1,3,5-isomer. 2,4-dichlorophenol, which may also be produced in the breakdown of BHC, causes similar deformation. The possibility of utilizing these materials in the role of selective weed killers is under investigation.

BHC preparations for cereal seed treatment against wireworms should be materials of high gamma content, applied at the minimum practicable rate for control. The hazards accompanying their use are likely to be increased by storage after treatment, especially if ventilation is inadequate, by exposure to sunlight, and by deficient moisture and high pH of the soil. Damage seems particularly likely to occur with Durum wheat; among oat varieties tested Larain suffered least damage, and among the barleys, Montcalm appears to have some resistance.

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EFFECTS OF ESTROGEN AND ANDROGEN ON LIVER IRON OF THE IMMATURE PULLET[1]

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INTRODUCTION

Sex is known to influence the storage and utilization of iron. Mitchell (9) showed that female rats had a higher blood hemoglobin than male litter mates and that females also took longer to become anæmic. Wakeham and Halenz (16) found that the livers of female rats contained a greater concentration of iron than the livers of male rats of the same age. Smith and Otis (14) found that hemoglobin regeneration was more rapid in female rats than in male rats. Otis and Smith (10) subsequently showed that the total iron per gm. body weight was greater in female rats than in males in spite of the smaller size of the female rats. Rose and Hubbell (12) found that female rats stored some 12 per cent more iron than males when the intake per gm. body weight was the same for each sex. The foregoing observations are all consistent with the idea that female rats have a greater capacity for storing iron than do males.

It was natural to suspect that gonadal hormones might be involved in determining such a tendency. Some years ago Steenbock *et al.* (15) reported that injections of estradiol benzoate (Progynon-B, Schering) into sexually immature female rats resulted in an increased storage of iron as compared with the storage by unestrogenized female litter mates. Steenbock *et al.* (15) did not furnish quantitative date in their report, but Widdowson and McCance (17) have recently published data relating to sexual differences in the storage and metabolism of iron in a number of vertebrate species. Widdowson and McCance (17) found that the livers of cockerels contained 8.7 mgm. inorganic iron per 100 gm. at twenty weeks of age, whereas the livers of comparable pullets contained 14.7 mgm. inorganic iron per 100 gm. liver. The variability of the data was large, but the difference between the average values for the sexes was statistically significant. The foregoing findings suggested that it would be of interest to explore further the possible effects of estrogen and androgen upon the iron content of the livers of the sexually immature pullet. The present paper deals with experiments made with this end in view. The possible effects on the copper content of the livers were examined at the same time.

EXPERIMENTAL

Method of Experiment

The experimental birds were sex-linked cross-bred (New Hampshire ♂ x Barred Plymouth Rock ♀) pullets. Two similar experiments were carried out. In each experiment sixteen birds were used. Each sixteen birds were distributed at random into four groups of four birds each and housed at random in individual cage laying batteries. Group A served as

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controls; Group B received androgen only; Group C received estrogen only; and Group D received both androgen and estrogen. The estrogen was estradiol benzoate (Progynon B, Schering) and the androgen was testosterone propionate (Oreton, Schering). Each treatment was divided into six equal doses which were injected into the breast muscles on alternate days over a twelve-day experimental period. The total amounts of oily base injected were equalized as between all the pullets. The levels of treatment are given in Table 1. The androgen treatment given to Group D was designed to produce a degree and speed of hypertrophy of oviduct and comb of the same order as that which takes place as the pullet enters normal reproductive activity. All birds in each experiment were given the same amounts of the all-mash diet (a commercial growing ration) so as to avoid effects due to differences in food intake. The birds were decapitated and bled on the second morning after the last injection, and the livers removed for analysis.

Analytical Methods

Total iron was determined by a slight modification of the A.O.A.C. method (1). About 1 gm. liver was ashed with sulphuric and perchloric acids and after suitable dilution an aliquot was taken for colour development using $\alpha\,\alpha'$-dipyridyl.

The inorganic iron of tissues corresponds to iron extractable from the fresh tissue by mildly acid solutions. It has been variously described as ionizable iron (13), available iron (4), inorganic iron (17) and free iron (6), and different workers have described different procedures for estimating this fraction of the tissue iron. For the purposes of the present experiments inorganic iron was determined by the method of Shackelton and McCance (13) modified for photoelectric colorimetry as follows:

About 0.75 gm. liver was weighed into a small mortar and crushed with a pestle. The liver was washed into a 25 ml. glass stoppered cylinder, using four 5 ml. portions of Walpole's acetic acid-sodium acetate buffer at pH 5.5 (5). The cylinder was then heated in a boiling water bath for ten minutes. After cooling, 0.5 gm. sodium hydrosulphite was added. The contents of the cylinder were mixed, and 2 ml. of 0.1 per cent $\alpha\,\alpha'$-dipyridyl was added. The cylinder was well shaken and left to stand overnight. Five ml. ethanol was added, the cylinder was well shaken and again left to stand overnight. The solution was filtered into a 100 ml. volumetric flask, and the cylinder washed out with distilled water. The residue on the filter paper was repeatedly washed with distilled water until a volume of 100 ml. was obtained. This solution was solution D.

At the same time three additional solutions were prepared. Solution A contained 20 ml. buffer, 0.5 ml. sodium hydrosulphite and 5 ml. ethanol. It was filtered and made to 100 ml. by washing the filter paper. Solution B contained the same amounts of buffer, hydrosulphite and ethanol plus 2 ml. 0.1 per cent $\alpha\,\alpha'$-dipyridyl and was similarly filtered and made up to 100 ml. Solution C was prepared in the same way as solution A, using 0.75 gm. liver, but omitting the addition of $\alpha\,\alpha'$-dipyridyl.

The Evelyn colorimeter was set at 100 per cent transmission (440 m u filter) with solution A, and solution B was read. This gave the photometric density due to reacting iron in the reagents and filter paper. The colori-

TABLE 1.—EFFECTS OF ESTROGEN AND ANDROGEN ON THE IRON CONTENT OF THE LIVER OF THE SEXUALLY IMMATURE PULLET

Average results for Experiments 1 and 2

	Group A	Group B	Group C	Group D
Number of pullets	8	8	8	8
Total dosage of extradiol benzoate, mgm.	Nil	Nil	18	18
Total dosage of testosterone propionate, mgm.	Nil	6	Nil	6
Initial weight, kgm.	1.01	1.03	1.01	1.08
Final weight, kgm.	1.22	1.24	1.22	1.23
Food consumption, kgm.	0.92	0.91	0.92	0.92
Liver weight, gm.	20.4	21.4	32.4	32.1
Liver inorganic iron:				
mgm. per 100 gm. liver	14.8	10.1	12.6	11.4
mgm. per liver	3.0	2.2	4.1	3.7
mgm. per kg. live weight	2.5	1.8	3.4	3.0
Liver total iron:				
mgm. per 100 gm. liver	18.4	12.8	16.0	14.9
mgm. per liver	3.8	2.7	5.2	4.8
mgm. per kg. live weight	3.1	2.2	4.3	3.9
Liver inorganic iron as per cent of total iron	81	79	79	77

	Least significant difference between groups (P = 0.05)	c.v. per cent
Liver inorganic iron:		
mgm. per liver	1.2	32.7
mgm. per kg. live weight	0.8	27.9
Liver total iron:		
mgm. per liver	1.5	31.4
mgm. per kg. live weight	1.0	29.1

meter was then set at 100 per cent transmittance with solution C, and the unknown solution D was read. This gave the photometric density due to reacting iron in the unknown plus reacting iron in the reagents and filter paper. The latter photometric density was corrected by deducting the photometric density due to iron in the reagent and filter paper.

The concentration of iron corresponding to this photometric density was then read from the calibration curve prepared by plotting iron concentration against photometric density of the $\alpha\alpha'$-dipyridyl complex. The reaction obeys Beer's Law for concentrations ranging up to 1.8 micrograms iron per ml. of final reaction mixture.

Copper was determined by digesting 1.5 gm. liver with 2 ml. concentrated sulphuric acid and successive additions each of 1 ml. perchloric acid until a clear digest was obtained. The solution was diluted and transferred quantitatively to a 100 ml. volumetric flask. The copper content of a suitable aliquot was determined by the method of Boulet and McFarlane (2).

Experimental Results

In the first experiment the pullets were 92 days old when killed and in the second experiment they were 103 days old when killed. Treatments and experimental procedure, however, were the same in both experiments Accordingly the data for the entire 32 pullets have been considered together and are presented in Table 1. The analysis of variance was made by the "split plot" method.

Variability of Liver Iron

The results reveal a fairly wide variability in both total iron per liver (c.v. = 31.4 per cent) and in inorganic iron per liver (c.v. = 29.1 per cent). This variability extended to both controls and treated birds. The data presented by Widdowson and McCance (17) also display a wide variability in the liver inorganic iron of both the pullets and the cockerels which they examined. The percentage of the total iron present as inorganic iron did not display such a wide degree of variability. It would appear that the iron content of the fowl's liver is subject to wide variation even in the case of pullets of the same strain and hatching and which have been reared under the same conditions.

Effect of Androgen on Liver Iron

A comparison of the data for Group A (control) and for Group B (androgen only) suggests that androgen tended to give smaller concentrations of both total iron and inorganic iron in the liver. Androgen also appeared to reduce both the total iron per liver and the inorganic iron per liver, and also the liver total iron per kgm. live weight. While none of these differences attained significance at the 5 per cent point, they approached such a level sufficiently closely to be regarded as on the borderline of significance. Androgen did not appreciably affect liver weight.

A comparison of Groups C (estrogen only) and D (androgen + estrogen) suggests that androgen evoked similar trends in liver iron in the presence of estrogen as well as in its absence; but here again the differences did not reach significance at the 5 per cent point.

Effects of Estrogen on Liver Iron

Estrogen increased liver weight by approximately 50 per cent. Estrogen also tended to decrease the concentration of both inorganic and total iron in the liver, but not to a significant degree.

None of the treatments gave significant differences in live weights or live weight increases and the live weights of all groups were sensibly the same. When the amounts of inorganic and total iron per liver are considered, it will be noted that estrogen (Group C) increased the mg. inorganic iron and the mg. total iron per liver, but that one difference from the controls (Group A) failed to attain significance. However, when the data were calculated on the basis of mg. liver inorganic and total iron per kg. live weight, then estrogen gave a significant increase over the controls.

Estrogen plus androgen (Group D) gave significant increases of liver inorganic iron and total iron as compared with androgen (Group B) whether calculated as mgm. per liver or as mgm. per kgm. live weight. Moreover,

estrogen also gave significant increases of liver inorganic iron and total iron as compared with androgen when calculated per liver as well as when calculated per kgm. live weight. It is clear from these results that estrogen increased the amounts of both inorganic and total iron in the liver.

Estrogen plus androgen (Group D) gave increases as compared with the controls (Group A), but these increases were smaller than the increases secured by estrogen alone (Group C) and did not attain significance.

The most reasonable explanation of the results as a whole is that the effect of androgen in bringing about a decrease of liver iron per liver and per kgm. live weight was real though not significant, and that this effect was exerted in the presence of estrogen as well as in its absence. Thus, when both hormones were administered together, the amounts of inorganic iron and total iron in the liver were intermediate between the amounts in the androgenized and in the estrogenized birds. Furthermore, although the treatment with estrogen plus androgen gave significantly greater amounts of total and inorganic iron in the liver than did androgen, it did not give a significant increase over the values for the controls. This fact, taken with the consistent trends of the average results, lends strong support to the foregoing explanation of the results as a whole.

The tendency for the concentration of iron in the liver to fall as a result of estrogen treatment is of interest. This feature of the results suggests that, in short-term experiments, hypertrophy of the liver may be relatively faster than the increase of storage of iron. It would be of interest to carry out similar experiments using more extended periods of treatment and lower levels of estrogen.

Effects of Estrogen and Androgen on Liver Copper

The effects of the hormonal treatments on liver copper were studied in the case of sixteen birds only (i.e., the livers from the second experiment). The results (Table 2), however, were sufficient to indicate that gonadal hormones do not affect liver copper to a degree comparable with the effects on liver iron.

TABLE 2.—EFFECTS OF ANDROGEN AND ESTROGEN ON THE COPPER CONTENT OF THE LIVER OF THE SEXUALLY IMMATURE PULLET

Number of birds	4	4	4	4
Total dosage estradiol benzoate mgm.	Nil	Nil	18	18
Total dosage of testosterone propionate mgm.	Nil	6	Nil	6
Initial weight, kgm.	1.08	1.07	1.11	1.11
Final weight, kgm.	1.25	1.26	1.28	1.26
Total food consumption, kgm.	0.90	0.91	0.91	0.92
Liver weight, gm.	21.3	22.0	33.6	33.7
Liver copper:				
mgm. per 100 gm.	0.58	0.47	0.34	0.34
mgm. per liver	0.11	0.10	0.11	0.10
mgm. per kgm. live weight	0.10	0.08	0.07	0.08

The results suggest a decrease in concentration of copper in the liver as a result of estrogen treatment; but when the data are expressed in terms of liver copper per kg. live weight, then there does not appear to be any difference between the copper contents of the livers of the control pullets and of the pullets receiving androgen, estrogen or androgen plus estrogen.

It may be observed that the copper content of an egg is of the order of one-tenth of the iron content. The results do not provide any evidence for the existence of copper reserves analogous with the inorganic iron of the liver.

DISCUSSION

In spite of the fact that some of the differences concerned do not attain statistical significance, the results as a whole afford strong support for the view that androgen tended to depress storage of iron in the liver, that estrogen increased storage of iron by the liver and that estrogen and androgen exerted their effects on the storage of iron by the liver independently. The results support the contention that the difference between the iron content of the livers of cockerels and pullets, as noted by Widdowson and McCance (15), is directly due to opposing effects of predominant androgen in the male and predominant estrogen in the female.

An average hen's egg contains about 2.3 mgm. iron concentrated mainly in the yolk (9) and there is little evidence that the diet of the hen has any effect on the iron content of the egg (7). Extensive data for the iron content of the fowl's liver do not appear to be available, and the principal studies relate to the changes in iron content during incubation (8). However, if it be assumed that the livers of the pullets examined by Widdowson and McCance (17) weighed about 50 gm. then these livers contained from 3.5 mgm. to 19 mgm. inorganic iron per liver. The inorganic iron is unlikely to represent less than about 75 per cent of the total iron (*vide* results of present experiments). The total iron content of their pullets' livers was, therefore, probably of the order of 4.7 mgm. to 25 mgm. iron per liver. It is thus evident that the iron requirements for egg production are fairly large in relation to the liver stores of iron. At the same time, and from a practical standpoint, McFarlane *et al.* (7) have pointed out that the possibility of nutritional anæmia in poultry, as a result of a deficiency of iron or copper in the diet, would seem to be extremely remote.

From the standpoint of iron metabolism in the pullet, it seems plausible to suggest that increasing estrogen activity will lead to an increased storage of iron in the liver as laying approaches. Any concurrent androgen activity will tend slightly to offset this influence, in contrast to the effects of androgen in relation to pre-laying storage of calcium in the pullet's skeleton (3). Furthermore, the amount of iron in the liver may well be subject to considerable fluctuations in relation to the demands for laying.

SUMMARY

1. The livers of immature pullets treated with estrogen contained significantly more total iron and inorganic iron per kgm. live weight than the livers of comparable pullets treated with androgen.

2. The livers of pullets treated with estrogen plus androgen contained significantly more total iron and inorganic iron than the livers of comparable pullets treated with androgen only.

3. The livers of pullets treated with estrogen only contained significantly more total and inorganic iron per kgm. live weight than the livers of comparable untreated pullets. Neither androgen alone nor estrogen plus androgen gave liver iron contents significantly different from those of the untreated pullets.

4. It is suggested that the results are most simply explicable on the ground that estrogen increases while androgen decreases storage of iron in the liver of the fowl, and that each hormone will continue to exert its influence on the storage of iron in the presence of the opposing influence of the other.

5. The copper contents of the livers of pullets treated with androgen or estrogen or both hormones did not differ appreciably from that of untreated pullets.

ACKNOWLEDGMENTS

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A FOUR-ROW POWER PLOT SEEDER

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In the dry area of west central Saskatchewan, served by the Dominion Experimental Station, Scott, the seed bed, in many springs, has a loose and dry surface with an underlying layer of hard clay, difficult to penetrate without power equipment. This condition in the spring had made it difficult to seed small grains deeply enough into moisture to ensure germination when using small, hand-operated nursery seeders. It is chiefly because of this soil condition in the spring that a decision was made to design and construct a power seeder in an endeavour to solve this soil-penetration problem. Other reasons influencing this decision were the difficulty of obtaining suitable extra labour for the short seeding period and the necessity of utilizing to the full the short period in the spring favourable for obtaining uniform stands of small grains in nursery plots.

In constructing the seeder, the following objectives were kept in mind:

1. To obtain sufficient penetration to place the seed in moist soil in the following types of seed beds: (*a*) those dry and powdery on top; (*b*) those difficult to penetrate because of clayey composition; (*c*) poorly prepared, trashy seed beds, and (*d*) seed beds on relatively new land containing clods and roots.

2. The seeding of four rows simultaneously to reduce labour costs and to speed up seeding operations.

[1] Cerealist, Substation Supervisor and Plotman, respectively.

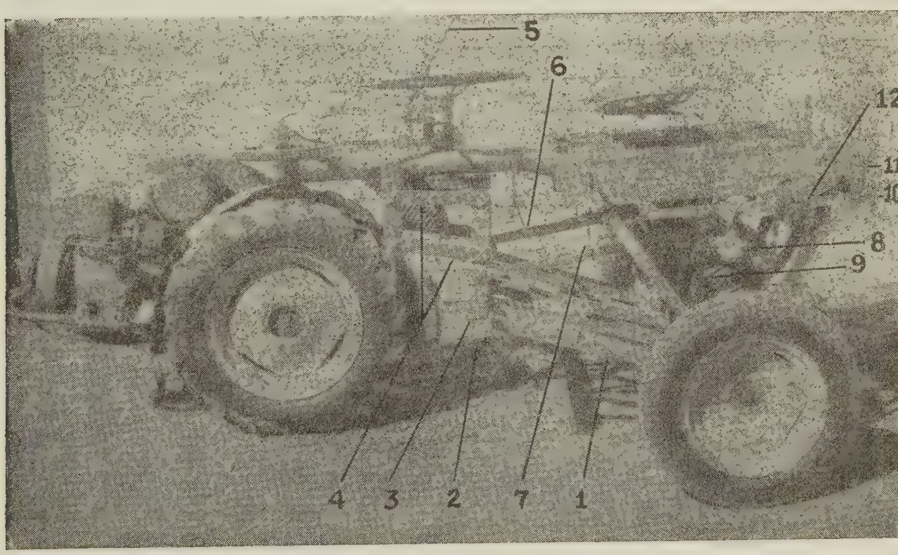

FIGURE 1. A side view with pertinent parts labelled. 1. Supporting arms. 2. Drawbolt. 3. Drawbar. 4. Arms for raising drawbar. 5. Pressure control lever. 6. Pressure arms. 7. Fulcrum of pressure arms. 8. Pressure bar. 9. Pressure springs. 10. Frame supporting V-belts. 11. V-belt unit. 12. 3/8 inch roller chain driving belts.

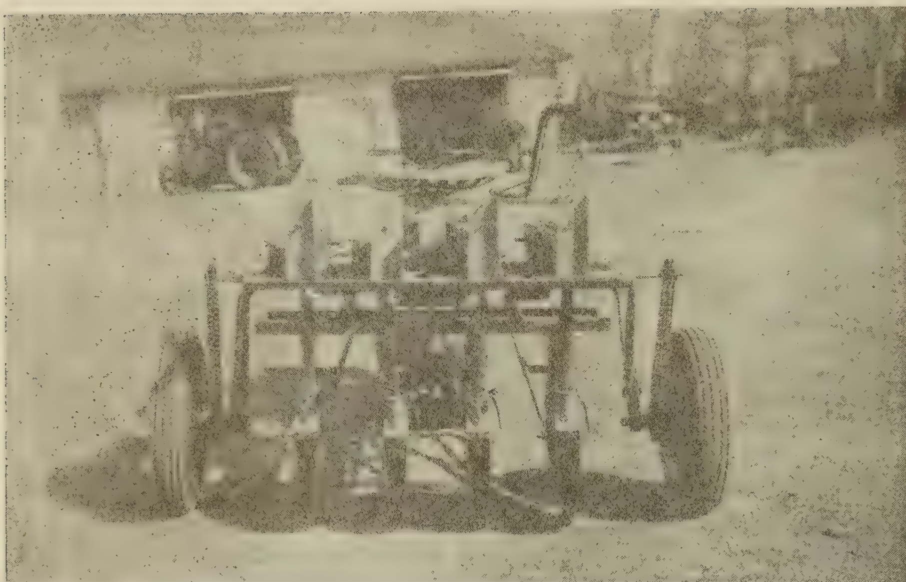

FIGURE 2. Rear view.

3. The use of four individual belts so that any desired type of plot i.e. single, two, three or four row plots, could be seeded.

4. Adjustable spacings for the furrow openers to seed nine-inch or foot spacings.

DESCRIPTION OF THE MACHINE

The assembled machine is shown in Figures 1 and 2 and different views of it in operation are given in Figures 5, 6, 7 and 8.

The 5 h.p. tractor was purchased. The double disk furrow openers with grain spouts, tension springs and supporting arms are the same as those used on a standard make of large grain drill. The V-belt attachment for delivery of the seed to the grain spouts consists of four Kemp (1) V-belt seeders, with wheels and handles removed, mounted on a $1\frac{1}{2}$ inch angle iron frame, 22 inches × 38 inches, above the disks. The distinguishing feature of the Kemp V-belt seeder is an endless rubber belt, shaped in the form of a "V". This belt is stretched over two steel rollers, spaced 20 inches apart, thus giving 20 inches of belt over which seed is distributed by hand. The portion of the belt covered by the seed depends on the length of row to be seeded. The ratio of the belt speed to ground travel is 1 foot to 12 feet. Thus, in seeding $18\frac{1}{2}$ feet of row, as is done in seeding a rod row, the seed is distributed over approximately 18 inches of belt. As the machine is moved over the ground the seed is carried by the belt to the conductor tube and thence to the furrow opener which places it in the soil. The V-belts which deliver the seed to the spouts are driven by a roller chain linkage from the hub assembly of the rear wheels to the axles of the V-belts. A chain on each side drives two V-belts. The lever and drawbar of the tractor are used to lower and lift the double disk furrow openers. This action is based on the fulcrum principle. As the drawbar is lifted, pressure is placed

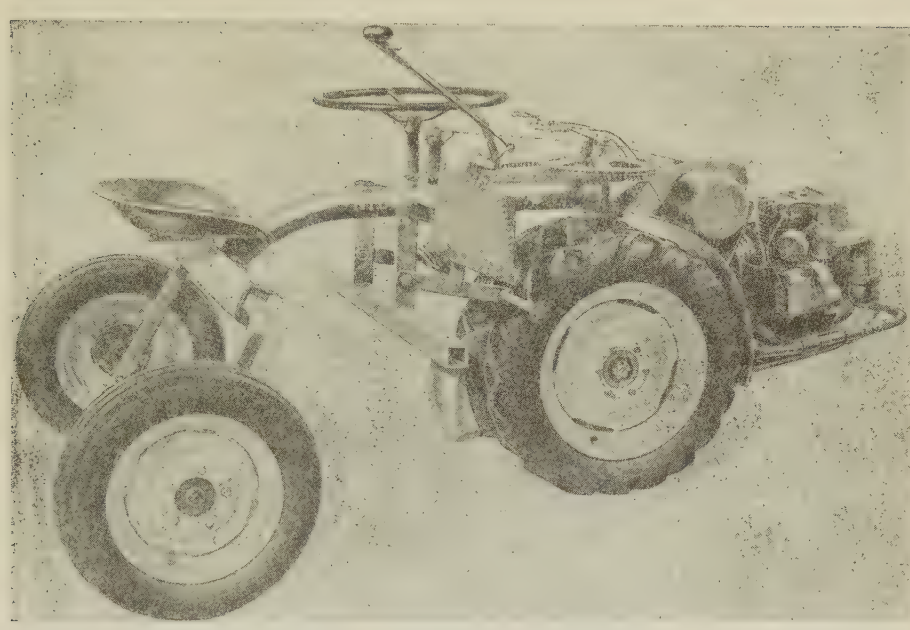

FIGURE 3. 5 h.p. riding garden tractor showing existing parallel linkage to tool-bar. The original tool-bar with two upright connections was replaced by the drawbar shown in Figure 4. The seeding attachment could be readily adapted to other styles of small 4-wheel tractors.

on the pressure springs to force the disks into the soil; as the drawbar is lowered, the disks are lifted clear of the ground. Figure 3 shows the tractor with original tool-bar.

An angle iron drawbar was made to take the place of the channel iron tool-bar which came with the tractor. Gusset plates were welded on to both ends and the middle of this drawbar and holes drilled in them through which a three-quarter inch rod was passed. This rod passed through the supporting arms of the double disk assembly to pull the disks. Three-quarter inch piping of appropriate lengths was used between the four supporting arms to provide different row spacings. On this machine, two spacings were used, viz., nine inch and one foot. Figure 4 shows this hook-up in detail.

The tractor is equipped with a multiple V-belt clutch which permits of instantaneous stopping and starting. After one season's work, seeding and cultivating, involving thousands of stops and starts, the clutch is still in first-class shape. When the clutch does wear out, replacement can be made easily and cheaply by the purchase of new V-belts. The machine is quite manœuverable. It reverses and can be turned in its own length, which is approximately six feet. Speed is controlled by the throttle.

SEEDING PROCEDURE

Seed for each row is placed in a single envelope and these are laid out on a table in the laboratory in exactly the same way as they will be seeded in the field. As the seeding is done straight across all the ranges of the

test, the envelopes are taken from the table for this manner of seeding in groups of four, stapled together and numbered in chronological order. The envelopes are then checked back with the field plan to see that everything is in order. When ready to seed, the groups of four envelopes are taken to the field and placed in the rack at the back of the drill in chronological order.

Six-foot pathways between ranges are marked out by driving a half-ton truck crossways every $18\frac{1}{2}$ feet. In cultivated ground, the tires make a wide, easily discernible mark. In this way, the marking-off of ranges is done quickly and efficiently.

One man drives the tractor, using the mark of one of the rear wheels as a guide. Two men feed the V-belts with the packaged seed, each feeding two belts. One man can feed all four belts; but it was found that relatively greater efficiency could be obtained by using two men for feeding. The machine is stopped in each pathway without lifting the disks while the seed is spread on the belts from the envelopes. The length of belt required for the length of row to be seeded had been calibrated previously and an inclined stop placed over the V-belt to mark the length of belt over which the seed is to be spread and to prevent any vibration on the belt. The drill is stopped in the pathway far enough back from the range mark so that when the machine is set in motion the first seeds drop at this mark. A little practice by the driver of the machine will enable him to stop at the proper spot in the pathway.

OBJECTIVES OBTAINED

This four row power nursery seeder has achieved the objectives in mind when it was constructed. Excellent stands were obtained when seeding was done in heavy clay loam soils, in soils which were loose and dry at the surface, in seed beds which contained a considerable amount of trash and in poorly prepared seed beds in co-operative tests with farmers. Figures 9 and 10 show stands at two different stages of growth.

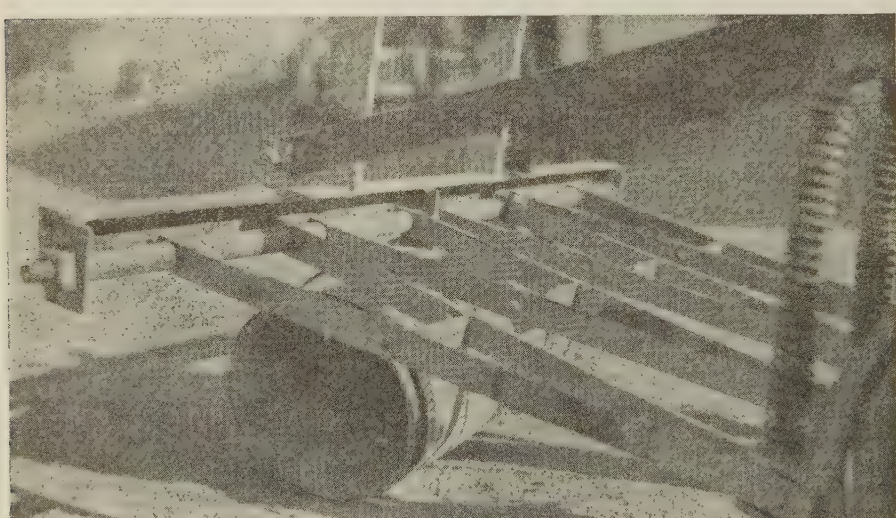

FIGURE 4. Details of hook-up of disk assembly to tractor drawbar (detached from tractor).

FIGURE 5. Two men feeding two V-belts each, and one driving tractor.

FIGURE 6. The drill half-way across a block of six rod row ranges.

FIGURE 7. A side view of machine in operation, showing depth of penetration of double disk furrow openers.

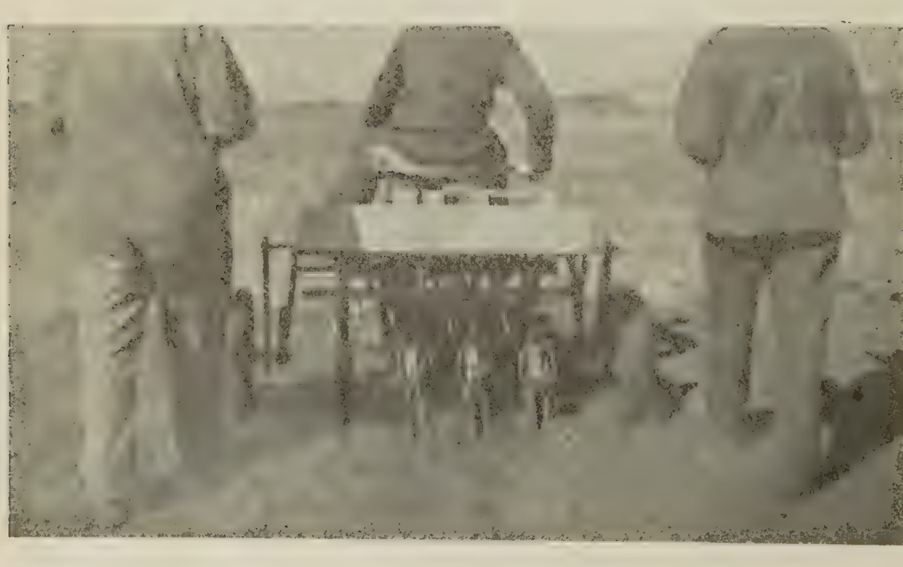

FIGURE 8. Rear view of machine in actual seeding operation.

FIGURE 9. Stands at Experimental Station, Scott, Sask., three weeks after seeding.

FIGURE 10. Stands at Experimental Station, Scott, Sask., five weeks after seeding.

Seeding was speeded up considerably and less labour was required. Previously, using three single-row hand-operated seeders, with two men to each seeder, six men seeded approximately 500 rows per hour. Using the power seeder and three men, from 500 to 600 rows were seeded per hour. Another desirable feature was the straightness of the rows with uniform spacings between rows, not usually obtained when single hand seeders were used. This proved a great advantage in weeding and harvesting.

SEEDING OUTSIDE TESTS

The seeder fitted quite nicely into a half-ton truck and was taken around the territory to seed outside tests. Its use resulted in a considerable saving of time away from the Station. A more important consideration,

however, was the ability of this seeder to seed into rough, trashy and difficult-to-penetrate seed beds often encountered on farms where the seed bed had been prepared well enough for the use of large machinery but not well enough for the use of small nursery seeders.

CULTIVATION

The drill can be quite easily and quickly detached from the tractor when seeding operations are completed and cultivator shovels or weeding blades attached for weeding purposes during the summer. A three-foot weeder blade has proven very satisfactory in cutting off and weeding six-foot pathways. Weeds were controlled satisfactorily without too much loosening of the soil and the pathways were left firm under foot, resulting in firmer and less dusty footing when taking notes.

SUMMARY

1. A four row power plot seeder has been described. Such a seeder was conceived and constructed mainly to avoid the discarding of many cereal tests due to poor stands in years when small, hand-operated seeders were not capable of placing the seed deeply and uniformly enough into moist soil.

2. A small 5 h.p. garden tractor was used as the source of power and a small drill, capable of seeding four rows simultaneously, was built to be attached to this tractor.

3. It was found possible, with this seeder, to seed into any type of seed bed and to obtain uniform stands.

4. The seeder was small and compact enough to be loaded into a small truck, transported around the country and used for seeding tests away from the station.

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EFFECTS OF RADIATION ON THE TEMPERATURES OF INSECTAN HABITATS[1]

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INTRODUCTION

During 1947, a program of meteorological observations was organized to investigate environmental situations of interest to those concerned with field problems of forest entomology. Data accumulated pointed up certain aspects of micrometeorology which, though not unknown, have not been assigned special importance in the past. This paper deals with one of these aspects—the effects of solar and terrestrial radiation on the physical conditions of insectan habitats and on the insects themselves. Prior to the development of the main theme of the paper, certain general points are outlined below.

Researches in ecological climatology with few exceptions have been directed towards analyses and assessments of the large and intensely localized differences in climates occurring within various types of cover or in areas of varying relief. Many investigations in this broad field have provided information of value to both biologists and meteorologists, but the somewhat standardized methods adopted have tended to minimize their value when they are applied to some entomological problems. Thus, the climate of the air surrounding a plant may be of very direct importance to that plant, but it does not necessarily follow that the same climate must have a continuously direct effect upon insects living upon or within the tissues of the plant. Therefore, there are times when data gathered by the usual methods may be definitely misleading.

Similar objections have been raised in the past (21, 22) and, in fact, led to a movement to study the microclimates of the actual dwelling places of insects. However, a subsequent broadening of the concept of microclimate has given rise to considerable confusion and, presumably, to the gaps noted between several laboratory analyses and attempts to apply them under field conditions. Under the heading of "microclimate", recent ecological literature appears to include everything from the humidity gradient above a transpiring leaf to observed variations of temperature among hill and valley stations, with the bulk of the investigations approaching the latter extreme. The impact of this new "microclimatology" upon entomology has led to adoption of some of its less precise techniques without serious consideration of the purposes for which they were originally designed.

Among entomologists, there is still a general tendency to assume that the temperatures of the various parts of plants, particularly the leaves, differ little from ambient temperatures. Yet, Curtis (5) has pointed out that plant surfaces during calm nights must be colder than the surrounding air; otherwise observed dew or frost deposition upon them would be hindered when air temperatures are above the dew point. Also, it was demonstrated (3, 4) that leaf temperatures rise well above those of the ambient air under the influence of solar radiation. This has been known to plant physiologists

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since about 1909 (for earlier references, see citations above), although at times there has been some disagreement among observers (cf. 24) as to the validity of the differences noted. Curtis (5) has covered these points adequately, and his arguments have the advantage of resting upon a sound physical foundation.

Plant physiologists have been concerned with this problem chiefly because of the possible influence of leaf temperatures upon transpiration. Nevertheless, examination of their data by an entomologist immediately raises the question of how such differences in temperature affect phytophagous insects during their development upon or within the plant tissues. Should these differences be considered in problems in which temperature is a factor, or are they small enough to be ignored and rejected in favor of thermograph temperatures? Since daytime differences measured by Curtis at times amounted to more than 10 Centigrade degrees, it would seem necessary to take them into account if they can be shown to occur in habitats of insects. Since many economically important insects feed exposed upon the surfaces of leaves, roll or web leaves, or mine within them or within vegetative buds, expanding shoots or fruits, the whole question seems worthy of serious consideration.

There is another point meriting consideration. Although it is not directly stated in standard texts, and despite some good evidence to the contrary (e.g. 9, 13, 23), it is frequently assumed that insects have body temperatures differing negligibly or not at all from those of their surroundings. Although this occasionally may be true under certain laboratory conditions, it seems to be an unwarranted assumption under a great many natural conditions. This and the previous points form the bases for the development of the present account.

LOCATION

Observations have been made at and near Sault Ste. Marie, Ontario. There is a possibility that some of the phenomena observed may be, in a quantitative sense, a function of latitude. Therefore, the reference line adopted is latitude 46° 30′ North. A tree in the grounds of the Forest Insect Laboratory was used as a point for winter observations; spring and summer observations were made at the Pointe aux Pins Insectary, the grounds of which contain disturbed second growth, in which *Pinus resinosa* Ait. and *P. Banksiana* Lamb. are co-dominant species, *Abies balsamea* Mill. and *Acer rubrum* L. are intermediate and suppressed species, and *Populus tremuloides* Michx. occupies openings among the pines.

EQUIPMENT

Standard "Stevenson" screen equipment was used in conjunction with a rain gauge in the insectary grounds. A barograph was kept in one of the buildings. Records obtained from these instruments were supplemented by visual observations of cloud amounts and types, together with wind velocities recorded by an anemovane-anemograph assembly. These general weather instruments were used to log frontal passages or air mass modifications.

Micrometeorological records were obtained with thermoelectric equipment. Leads of either number 24 or 30 copper-constantan glass-insulated duplex wires were used. Various reference-bath temperatures were employed, depending upon the type of investigation and upon the type of ambient conditions encountered. Thermojunctions were calibrated against each reference temperature. For field use at a permanent installation, an ice bath has little value. In some thermometric work (2), it had been found useful to immerse the cold junction box in a bath of transformer oil contained in the well of the bulb of a mercury thermoregulator. This, when used in a larger bath, provided a steady reference temperature near room level. On the basis of this idea, it was decided to use a reference bath heated to a temperature above any which might be encountered in the field and attach the reference junction to a regulator bulb in much the same way as that noted above. Apart from providing a reference temperature which was steady and quite independent of field conditions, this also had the advantage that all temperatures encountered were on one side of the reference temperature, an important item in continuous recording. Since all temperatures were below that of the reference, it was necessary to reverse the polarity of the thermocouples to obtain records.

The bath currently in use was constructed by J. M. Cameron to meet the above specifications. Glycerine was used as the bath fluid, to avoid undue losses, and a steady reference temperature of 58.4° C. was obtained by using a "Chromel" coil heater enclosed in a glass tube, and a mercury switch, which operated the heater through a relay. This equipment has given excellent service. Since early 1948 no additional glycerine has been required, and, apart from occasional chatter in the relay, which can be readjusted, no servicing has been required.

Single-junction couples have been used in preference to thermopiles, since the latter are too much affected by radiant energy. Satisfactory sensitivity was obtained by modifying the meters noted in a succeeding paragraph. Both individual and multiple sets of leads have been used. When multiple circuits were employed, they were arranged to work through a single reference junction, and this arrangement has given no trouble to date. Paired wet and dry thermocouples (cf. 15, 18, 20) have been used on occasion to determine atmospheric moisture levels in restricted spaces having little or no air movement.

Two types of potentiometers were used. A portable, dual-range potentiometer was used for "spot" indications in conjunction with either an internal or a highly sensitive external galvanometer, as the occasion demanded, and a multiple-point, recording potentiometer was employed to obtain 24-hour traces of the fluctuations of several variables on a single chart. A maximum number of 12 different leads could be employed with this instrument, with one junction being recorded every 30 seconds. Thus, although a truly continuous trace was not obtained for individual junctions, a variable at any point could be recorded every 6 minutes, when all contacts were in use, or more frequently, by short-circuiting some contacts, when fewer than the set of 12 were needed. This instrument was modified by resistor changes to reduce its full-scale reading from 15 to 3 millivolts. This gave a very open scale with single-junction leads.

A thermoelectric pyrheliometer was used to obtain records of radiation during daylight. When the instrument was attached to a recording potentiometer, continuous records of the fluctuations of radiation under cloud covers of varying densities were obtained. In addition, simple apparatus for recording temperatures similar to those found on some plant surfaces was employed in 1948 and 1949. This has been noted elsewhere (27). The thermograph employed for this project can also be combined with another, on the black-and-white element principle (12), to record nocturnal cloud, if such measurements are required.

METHODS AND MATERIALS

Much of the microclimatic work was directed towards collection of data on the "surface" temperatures of various parts of trees. A comment on "surface" temperature is necessary at this point. Measurements of the true temperature of any surface cannot be obtained thermoelectrically, since the junction is affected both by the temperature of the surface of the object and by that of the surrounding air. Apart from these factors, introduction of the junction into the system has a rather undesirable influence. Thus, unqualified references to a "surface" temperature are to be shunned. Nevertheless, the measurements obtained do give an approximation of conditions both at and near the surface of an object, as opposed to conditions in the air outside the boundary layer about it, and, if they are accepted in this light, they are very useful for comparative purposes. It is in this sense that "surface" temperatures are discussed in the following pages.

When surface temperatures of foliage were to be recorded, junctions were attached in several ways, depending on the type of measurement required. Measurements of the temperature of an aspen leaf, for instance, could be obtained by threading the wire through the leaf so that the junction was in contact with the desired point on the surface. Measurements of the surface temperatures of twigs or of the needle bases of conifers were made by running the lead along the long axis of the twig to the point desired, and tying it at two points well back from the junction with short lengths of number 30 resistance wire. The junction was then pressed into position in contact with the surface. Measurements of the temperatures of the interiors of needles, vegetative buds or staminate flowers were made in the same way, the free junction being inserted into the part of the tree to be measured.

Measurements of the temperatures of the interiors of buds or needles also are subject to errors, which, in this instance, stem partly from temperature differences in the leads near the junctions. Although such errors may be avoided or minimized if the object to be measured is large enough (6), they are difficult to eliminate when very small objects are being investigated. Once more, the comparative value of such observations must be stressed over the degree of accuracy obtainable. In short, if two temperatures are being recorded in different objects by matched thermocouples under the same ambient conditions, and large differences in temperature are observed, the fact that an actual error of 0.5 Centigrade degrees is operating in the same direction in both readings is relatively unimportant.

Errors of thermocouples due to radiation are more common than is generally admitted, and are difficult to eliminate. The best approximations to actual temperatures may be obtained with the smallest wire diameters practical for the problem at hand, and with the use of suitable shielding. In the present work, the leads were shielded from undue effects of radiation by wrapping them with aluminum foil for a distance of 10 cm. back from the junctions. Air temperature junctions were further shielded from direct sunlight and from the night sky by 5 cm. squares of foil mounted 10 cm. above the junctions. If all junctions are matched to uncover possible differences stemming from faulty contacts or other circuit defects prior to their use in the field, radiation errors may be assessed. If doubts arise as to the validity of foliage temperatures taken with exposed couples, it is best to expose a similar couple nearby to record unshielded air temperature, and to compare both readings with those taken by a shielded air temperature junction at the same level and orientation. Sometimes it may be advisable to make a further check by taking the air temperature at the level with the dry bulb of a calibrated sling psychrometer.

Such checks uncover effects of radiation. If the supposed foliage temperature measured by the first junction was largely a result of radiant heating or cooling of the junction, the unshielded air couple should register very similar results. Both readings should fluctuate quite consistently together and be out of phase with fluctuations of the air temperature measured by the shielded junction. On the other hand, if the greater portion of the reading given by the foliage junction actually resulted from energy communicated by the foliage, a difference between the foliage and air junctions will be noted, and the fluctuations of the exposed air junction will approximate those of the shielded one. This, incidentally, should not be taken to mean that temperatures of air and the objects surrounded by it should never fluctuate in the same direction when the objects are influenced by radiation. Such fluctuations do occur. The point made above refers specifically to the testing of direct effects of radiation on the thermocouples, and independent short-period fluctuations, if at all persistent, are good indications of a reasonable lack of such influence. In the present work, direct influences of radiation on the junctions and nearby leads were reduced to 0.2 Centigrade degrees.

When junctions are attached to portions of a tree in order to compare its foliage temperatures with those of another species, it is necessary to keep both sets of junctions as close to the same level as possible, and also it is desirable to attach them to points having the same orientation. Since it is sometimes impossible to fulfil both these requirements under field conditions, slight positional differences at times tend to obscure relationships. Interpretation of records, therefore, first calls for comparisons of the daily curves from which differences which occur consistently at fixed times may be identified. If these are found, the orientations of points in the installation must be checked and movements of surrounding shadow patterns must be determined. A final check of this type is always necessary before a temporary installation is destroyed or moved elsewhere.

Preliminary observations have been made on specimens of aspen (*Populus tremuloides*), balsam fir (*Abies balsamea*), jack pine (*Pinus Banksiana*), white spruce (*Picea glauca* Voss) and on a specimen of blue spruce

(*P. pungens* Engelm.). Although this list is far from complete, the data accumulated, when considered in relation to previous work (10, 14, 16) provide good bases for more intensive investigations. As noted previously, surface temperatures of foliage and of the bark of twigs have been observed, together with internal temperatures of vegetative buds, expanding shoots, staminate flowers, leaf rolls constructed by a tortricid on aspen and webbed tunnels of the spruce budworm, *Choristoneura fumiferana* (Clem.), fashioned in expanding shoots of balsam fir. In connection with other work directly concerned with the spruce budworm (26), body temperatures of larvae of the final stage were measured in relation to tunnel temperatures and air temperatures, and some of these data are incorporated as illustrative material. In addition, some measurements of the web temperatures of tent caterpillars, *Malacosoma* spp., and of the fall webworm, *Hyphantria textor* Harr., have been obtained during an investigation still in progress, and some examples of these are included.

RESULTS

The observations reported below have been arranged to follow a seasonal trend as closely as possible, in order to demonstrate degrees of differences of microclimates peculiar to definite periods of the year at higher latitudes. Where possible, variations stemming from conditions associated with daylight and darkness and from the presence or absence of cloud or precipitation are noted. It was thought best to present as much of the data as possible in the form of extreme differences rather than in the form of lengthy tables. As may be seen from the few illustrations included, the extremes listed are not merely momentary occurrences but persist over lengthy intervals.

Winter

The first series of observations of entomological interest was complied during the winter. The series was begun to investigate the possible importance of tree-borne snow to stages of various insects overwintering upon or within the twigs of trees. Although the moderating influence of ground-surface snow cover upon the temperatures of underlying soil is well known, and its significance to insects overwintering there has been pointed out (17), the effects of snow attached to the branches of trees upon the surface temperatures of those branches has been an open question. On theoretical grounds, the snow should exert a moderating influence, by virtue of its powers of reflection during sunlight and its properties of insulation at all times, just as it does on the ground. Nevertheless, examination of snow-covered conifers shows that, while snow on the upper surfaces of branches might accumulate to depths of 20 cm. and remain in place under sheltered forest conditions, penetration of the snow through the spaces between twigs is poor, usually amounting to less than 3 cm. Thus, except when two snow-laden branches become fused within a common mantle of snow, the under-surface of a branch would appear to be poorly insulated and subject to penetration by cold air currents. Direct measurements were required to clarify the situation.

Thermojunctions were attached to twigs of an isolated Colorado spruce standing on the snow-covered lawn about 8 metres to the south of the

laboratory. A more rigorous test of the efficiency of snow cover could scarcely have been devised, since the tree was exposed to direct sunlight and stood in a wind channel some 25 metres wide, directly in the path of the prevailing winter winds. Junctions were applied directly to the upper surfaces of the bark of terminal twigs, so that measurements of temperature at needle bases could be obtained. One twig was kept free of snow, while another at the same level and approximately the same orientation was kept covered with 8 to 10 cm. of snow, the lower surface of which finally adhered to the needles and protruded 1 cm. beneath them, the whole remaining in place even at relatively high wind velocities. Air temperature at the same level was recorded by a separate junction midway between the two "foliage" junctions. Both potentiometers were used at different times to obtain records. The results are summarized below.

During the daylight hours, the snow cover on the branch reflected some solar radiation. With air temperatures ranging from −15 to 0° C., the temperatures of the snow-covered foliage ranged 0.5 to 3.5° below the air temperatures under clear skies, broken cloud or thin overcast, with the larger differences occurring during the hours of maximum insolation. Strong winds did not appear to diminish the differences appreciably. No indication of undue absorption of radiation by the junction through the snow (cf. 8) was noticed, possibly because the lead diameters were smaller than those ordinarily used in snow temperature measurements.

By day, the exposed foliage usually exhibited temperatures in excess of those of the air, indicating a marked amount of radiant heating even at the low solar altitudes of winter. Maximum elevations above the ambient temperature which were noted in clear weather approached 2.2°. Thus the exposed foliage was, on occasion, over 5° above the snow-covered foliage. These differences in temperature were subject to rapid fluctuations, but, in sunlight, the variations were never accompanied by a change in the sign of the difference. The exposed foliage was warmest, with the air at an intermediate temperature and the snow-covered foliage at the lowest temperature. Under thin cloud, sufficient radiation penetrated to maintain the exposed foliage 1° or less above air temperature. Under dense cloud, the difference was negligible. When an isolated cloud obscured the sun, but left the overhead sky clear, radiation losses lowered the temperature of the exposed foliage 1° or less below the air temperature. It is interesting to note that with winds of 28 to 33 m.p.h. (13.9–17.1 mps.), the exposed foliage was still warmed 1–2° above the ambient temperatures by radiant heating.

The reverse situation occurred by night. Under nocturnal conditions within the polar continental air masses common to the interior of North America in winter, the surface of the earth and the exposed objects upon it radiate freely to the upper air. The surfaces follow approximately the laws of black-body radiation, and since their temperatures, however low, are warmer than those to which they radiate, surface temperatures fall well below the temperature of the air immediately surrounding them. Under such conditions, air temperatures near the surface follow the surface temperature, largely by conduction and extremely slow convection, rather than the exposed surface taking up the temperature of the air, as at first

thought one might expect. The net result, if measured as air temperature, is revealed in the presence of a surface inversion, within which air temperature increases rather than decreases with height (25).

This situation proved to be of importance to the results being described. Under clear skies, and with little air movement, the snow-covered twig remained warmer than either the air or the exposed foliage, since its snow cover insulated it rather effectively from direct conduction from the surface layer of air and also, to a certain extent, retarded its radiation. Although radiation took place, its rate was slower than that from the surface of the exposed foliage, which, because of its loss of heat by outgoing radiation, cooled below the ambient air temperature. Under the above conditions, snow-covered foliage was 0.5° warmer than air at −20° C., or 1.7° warmer than air at −15° C., whereas, at the same times, exposed foliage was 0.3 to 0.8° cooler than the air, or 0.8 to 2.5° cooler than the snow-covered foliage. The ranges noted above are small, but indications are that they might have been increased in a more sheltered situation. The wind channel mentioned previously proved to be particularly troublesome at night, when it became part of a local situation which was meteorologically interesting, but a hindrance to attempts to determine effects of radiation on the temperature of various surfaces.

On "good" radiation nights, a street down a low hill to the north of the laboratory acted as a channel through which air chilled by radiation on the hill top moved in much the same manner as katabatic winds move down slopes or funnel along valleys at night. Buildings along the street channeled the air, and, towards midnight, a 7 to 10 m.p.h. wind (3.4-5.4 mps.) had developed which entered the wind channel in which the tree stood, thus breaking down the radiation pattern in that area. This occurred even on nights when strong inversions were forming in other parts of the town, as evidenced by the layering of chimney smoke at moderate elevations. Yet, although troublesome, this wind did show the destructive effects of even slight air movement upon nocturnal radiation proceeding at a low temperature level.

In experiments upon the relation of leaf temperatures to transpiration (3), it has been mentioned that leaves radiate to temperatures below that of the air even when strong winds are present. As it stands, this statement is incomplete. It should include a notation to the effect that leaves do so *if* their temperature level is high enough. According to the Stefan-Boltzmann law, the rate of radiation decreases when the temperature of the body decreases. Thus, a wind speed which is not sufficient to disrupt completely radiation from a leaf surface at high summer temperatures will be more than adequate for the purpose at low winter temperatures, because the rate of radiation is considerably less at the lower temperatures.

Accordingly, wind speeds of about 2–3 mps. were sufficient to break down the radiation patterns at the temperatures of −12° C. or less which were common during the observational nights. Since these winds, although intermittent, occurred frequently, inspection of the data suggests that maximum differences between the temperatures of the air and the exposed foliage were seldom, if ever, attained. Nevertheless, the differences which were observed did indicate real variations in the rates of radiation at dif-

ferent temperature levels. The difference of 0.3° was recorded in the air temperature range of −20 to −23° C., whereas the 0.8° difference was observed in the range from −15 to −18° C. Calculation of the percentage decrease of flux per Centigrade degree decrease of temperature shows a continuous decrease in the rate of heat loss by radiation over the range from +60 to −60° C. and indicates the interesting possibility that, at temperature levels below approximately −30° C., which are not at all unusual in the northern forest region, the difference between the temperatures of exposed foliage and its surrounding air might be negligible for practical purposes, even when undisrupted radiation is in progress.

Although wind disrupted differences observed between air and exposed foliage, and tended to eliminate them, it also exposed the chief weakness of tree-borne snow cover on an isolated branch. The lack of a sufficiently thick insulating layer on the under surface of a branch permitted penetration by turbulent currents, so that the temperature of the snow-covered twig also approximated that of the air at moderate wind velocities, being lowered by the penetrating air.

The presence of nocturnal cloud changed the relationships described above according to the density and uniformity of the cloud cover. Thin, high stratiform cloud exerted a negligible influence, diminishing differences by a barely observable amount, and broken cloud exerted little more influence. On the other hand, an overcast of low, dense stratiform or cumuliform clouds reversed the sign of the difference between temperatures of exposed foliage and the air. Under such conditions, even with the low prevailing temperatures, the exposed foliage absorbed sufficient quantities of reflected and re-emitted radiation coming from the clouds to have its temperature raised up to 0.3° above that of the surrounding air. Lifting of the cloud base or thinning of the cloud was characterized by an immediate decrease in this difference. The foliage temperature once more approached that of the air, and, with clearing skies, dropped below it again. Snow-covered foliage usually was maintained at a temperature about 0.5° above the air under an overcast.

The results described above indicate the moderating influence of tree-borne snow cover upon the temperatures of underlying twigs and foliage. Since the differences are presented in Centigrade degrees, they appear to be rather small, and, in comparison with temperature differences existing between the top and bottom of a layer of snow on the ground, they are. Nevertheless, viewed from the standpoint of the wide fluctuations in environmental temperature experienced by an insect overwintering on a tree, the differences may be important to survival. Translated into terms of the daily march of temperature, they mean that an insect on a branch covered by a light layer of snow would, while air temperature moved through a 23° range in a day and a night, be subjected to temperature fluctuations ranging through 17 or 18°. An insect on a fully exposed branch would be subjected to fluctuations through a 26° range during the same period. When generally low temperatures prevailed, the stress imposed upon the ability of the exposed insect to acclimate rapidly, or upon its ability to withstand temperatures near its lower lethal range, might be of considerable importance to its ultimate survival.

It should be remembered that the foregoing observations were made on a tree having the maximum exposure to winds. The effects of surrounding trees upon the retention of snow cover by conifer branches is very great, and field observations indicate that all but the most exposed portions of the crowns retain the bulk of freshly fallen snow during most of the period of cold, clear weather characteristic of winter polar air masses interjected between periods of snow-fall, so that, except during actual thaws, the supply of snow in the crowns of a moderately dense stand is maintained and replenished. Thus, the vertical distribution of a population over-wintering on a tree becomes of importance, if any statements based on laboratory determinations of lethal temperature ranges are to be extended to cover field conditions.

Snow retention by the branches of deciduous trees is much less than in conifers. This appears to be a result not so much of the lack of surface area for snow retention but of the greater reaction of a whole tree to wind action upon its top, if this is at all exposed to wind. Vibration and shearing in such circumstances account for a greater portion of the snow lost. It has been noticed that smaller deciduous trees partially overtopped by other trees retain a light snow cover along the upper surfaces of the branches, and frequently retain balls of snow 20 cm. thick in the regions of the forks. The type of snow is also important where deciduous trees are concerned. During the winter of 1947-48, much of the snow which fell in the vicinity of Sault Ste. Marie was powder snow, which was scarcely retained by deciduous trees. During the winter of 1948–49, the majority of the snow types consisted of stellar crystals, hexagonal plates or graupel forms (19) and falls of these types remained on main branches which did not retain powder snow.

In closing this sub-section, it may be noted that in lower latitudes, with milder winters and higher values of insolation, daytime discrepancies between air and tree temperatures will be increased considerably. For instance, a recent research note (1) gives differences of about 26° in favour of cambial temperatures on the sunlit side of a tree at air temperatures near 7° C.

In connection with insects themselves, rather than with their over-wintering sites, the only available material on which direct measurements could be made has been egg masses of the forest tent caterpillar, *Malacosoma disstria* Hbn. During February, 1949, records were taken of the temperature on the upper side of a mass, just beneath the protective layer of material covering the eggs. A specimen set of observations is shown in Table 1. The measuring equipment had no apparent ill effects upon the eggs, for they hatched outdoors in late April, 1949.

Spring and Summer

The following descriptions are applicable to the period covered by the months, May through August. In the first sub-section on general trends, results are presented in summary form only, by citation of extremes noted, as in the bulk of the descriptions of winter events.

General Trends

Diurnal Observations

Clear Sky

During daytime in the first week of May, surface temperature of blue spruce foliage of the previous year's growth was raised 2.8 to 5.6° above the temperature of the surrounding air, when the air temperature ranged between 12.8 and 15° C. When the foliage was shaded from direct sunlight, but remained exposed to a clear sky, its temperature ranged from 0.8° above to 2.2° below the air temperature. The intervals during which the shaded foliage was above the air temperature were very brief, coinciding with movements of the over-topping foliage which permitted some penetration of solar radiation.

In the direct sunlight of late May, the surface temperatures of the needles and expanding vegetative parts of the coniferous species tested tended to be very similar to one another under conditions of uniform elevation and orientation. Moreover, the temperature of air enclosed by an aspen leaf rolled by a tortricid larva also approximated the temperature of the types of foliage noted above. On the other hand, normal aspen leaves had temperatures which were markedly lower than the other temperatures observed. All foliage temperatures were above ambient ones in sunlight.

The difference between normal aspen leaves in sunlight and the needles or vegetative buds of the coniferous species was apparent in all records examined. At air temperatures between 15 and 26° C., aspen leaves

Table 1.—Internal temperatures, in centigrade, of an egg mass of *Malacosoma disstria* Hbn. during a twenty-four hour period

Time: EST.	Air temp.	Δ Egg temp. — air temp.	Weather notes
0000	−11.5	0.2	Moderate snow; wind 15-20 m.p.h.
0100	−12.3	0.1	Clearing; wind dropped to near calm
0200	−11.1	0.0	
0300	−12.3	−0.3	
0400	−13.4	−1.0	
0500	−14.6	0.2	Cloud patch
0600	−14.8	−0.7	
0700	−15.6	−1.0	Greatest negative Δ at 0630, −1.3
0800	−15.5	−0.1	Isolated stratiform patches
0900	−14.4	−0.9	Cloudless; hazy (eggs shaded)
1000	−10.6	0.0	
1100	−12.0	1.6	
1200	−11.0	3.4	
1300	− 9.0	4.9	Stratiform cloud on horizon; largest positive Δ, 5.3 at 1330
1400	− 8.6	−0.5	
1500	− 8.5	1.9	
1600	—	—	
1700	− 7.9	0.4	Overcast altostratus from 1530
1800	− 8.2	0.0	Overcast altostratus
1900	− 8.8	−0.2	Overcast, thinning
2000	− 9.5	−0.1	
2100	− 9.5	0.0	Overcast, thickening
2200	− 8.7	−0.2	Overcast
2300	− 7.3	−0.1	Overcast
2400	− 6.0	−0.1	Overcast

ranged only 0.5 to 1.6° above the air, whereas coniferous foliage ranged from 1.6 to more than 8° above the air, usually being maintained at least 5° above air temperature. Closer examination of the situation indicated that this discrepancy between the broad-leaved tree and coniferous species might result not so much from the continuous movement of the aspen leaves, since whole conifer branches were often in motion during the same periods, as from the angle at which the deciduous leaves were presented to the rays of the sun. All conifers, even jack pine, presented surfaces more closely perpendicular to incoming radiation than did aspen. It may be doubted that the angle of incidence could have such a profound effect, but further evidence exists in data obtained in the aspen leaf-roll. Tortricid larvae drew pairs of aspen leaves together in such a way that each pair projected outward at an angle of about 40°, instead of hanging almost vertically as did normal leaves. As noted above, the temperature of the air enclosed by these rolls approximated that of the surfaces or the interiors of coniferous foliage.

During the summer, surface temperatures of coniferous foliage exposed to direct sunlight moved through approximately the same range above air temperatures as was noted in the preceding paragraph, although there was some tendency for average values to remain a fraction of a degree higher than those noted for late May. On the other hand, when the foliage was shaded from direct sunlight, but remained exposed to the sky, its temperature dropped 1 to 3° below the air temperature, when this was in the vicinity of 30° C., as opposed to the maximum drop of 2.2° noted for spruce in air at 15° C. Strong winds exerted no readily observable influence upon the foliage or bud temperatures during hours of sunlight.

Clouded Sky

Introduction of clouds into the system produced a number of complications in the foliage-air temperature daylight relationships. Seasonal differences in cloud structure related to seasonal trends in air mass types also exerted recognizable influences upon the relationships.

During early May, thin, stratiform clouds, such as cirrostratus, or broken clouds, such as altocumulus, were high enough and thin enough to allow the passage of enough insolation to maintain fully exposed foliage 2.8 to 3.9° above air approximating 15° C.; a reduction of only 1.7° in the maximum elevation of temperature under clear sky. During the whole month of May, scattered cumulus clouds over the area were a turbulence type of fair-weather cumulus (Figure 1) and were neither slow enough nor sufficiently developed vertically to exert any appreciable influence. Under a broken sky, foliage which was shielded by other foliage from the sun but not from the sky received sufficient cloud-reflected radiation to maintain its temperature about 1° above that of the air, in direct contrast to the comparable situation under a clear sky. Under a heavy overcast of either stratiform or cumuliform clouds, all foliage was maintained about 1° above air temperature by diffuse radiation. The latter result differed from the observation under heavy diurnal cloud in winter. The difference resulted from stronger summer radiation.

During the summer months, further information on the relation of cloud types to foliage temperatures was obtained with the pyrheliometer.

FIGURE 1. Low-level fair weather cumulus, turbulence type, *circa* 500 meters altitude, moving from the west with a surface wind of about 20 m.p.h. (8.9 mps.).

In the records, several examples of sudden, brief reflections from passing individual clouds occurred, which added momentarily to the total radiation value recorded. These "zooms" (cf. 11) are of uncertain meteorological significance, but are definitely of no importance to foliage temperatures, since their periods of occurrence are too brief to bring a response.

As in May, scattered cumulus cloud moved too rapidly to have much influence upon the foliage. Judging by the records, if the period of fluctuation of the intensity of radiation was less than 3 minutes, no observable effect occurred in the foliage temperature. A period of serious depletion of solar energy more than 3 minutes in length, such as occurs when the towering portion of a heavy cumulus passes overhead, resulted in radiant cooling of the foliage, to or below the level of the air temperature. On the other hand, when stratiform cloud appeared on summer mornings, foliage temperatures averaged 2° above air temperature, as compared to 1° in May.

It was observed that, whether the insolation was rising or falling in value, swings superimposed upon the trend gave comparable swings in foliage temperatures. A total swing of 1.1 to 1.3 gm. cal./$cm.^2$ gave a swing of about 6° in foliage temperature; 0.7 to 0.9 gm. cal. fluctuations gave a foliage fluctuation of 4°, and 0.2 gm. cal. fluctuations gave swings in foliage temperature amounting to about 1°.

Rain

When rain fell, the differences between the temperatures of the air and the trees were of either sign, but were negligible. On the other hand, as soon as the rain stopped, evaporation from raindrops resting on the foliage lowered its temperature as much as 2.8° below that of the air for as long as 40 minutes.

Nocturnal Observations

Clear Sky

The phenomena observed at night depended partly upon the weather of the afternoon and partly upon the weather during the night. If a clear day was followed by a clear night, during which there was little or no air movement, both the air and the various foliage temperatures fell to low values. In May, air temperatures usually dropped to the vicinity of 0° C. during such nights. Radiant cooling of all types of foliage lowered their temperatures 1 to 1.2° below the air. When the air temperature fell only to 4.5°, the foliage cooled 1.6° below the air.

Fog occurred often between 2200 and 2300h. on clear spring nights. About 10 minutes after fog was noticeable, a sudden drop in temperature occurred which once amounted to almost 4°. However, as the fog thickened, the air temperature rose slowly, presumably because of heat liberated by condensation, and the foliage temperatures gradually rose towards the air temperature, since the fog droplets absorbed and re-radiated most of the original outgoing radiation. If the fog suddenly dissipated, within 10 minutes of its disappearance a second drop in temperature occurred, and radiant cooling of the foliage increased the difference between the temperatures of air and tree once more.

During clear summer nights, when the air was in the neighbourhood of 10° C., if it was calm, all foliage temperatures dropped as much as 3° below the air temperature. Strong inversions of temperature occurred in the lower air on such nights. No upper air moisture data were available, but it was noticed that on other nights which appeared to have no more air movement, radiation decreased the tree temperatures to only 1° below air temperatures, and, in the lowest layers at such times, only weak inversions or isothermal conditions were present. While this occurred often with some air movement, its occasional occurrence under apparently calm conditions suggested the presence of increased water vapour content of the air above the station at such times.

Clouded Sky

If afternoon cloud dissipated before or shortly after sunset, the conditions noted above for a clear night prevailed and the same differences were observed. If clouds persisted into the evening, radiation from nocturnal cloud-types was not sufficient to maintain the foliage temperatures more than 0.1° above the air temperatures during spring and summer. In fact, a dense, stratiform overcast was required to maintain any vestige of equality between air and tree. This was in contrast to the situation observed during winter. Lifting or breaking of night clouds was indicated by a sudden cooling of the foliage until the differences previously indicated were reached.

While foliage differences, such as that noted between normal aspen leaves and coniferous foliage occurred during the day, no such difference was observed at night. Apparently radiation from the trees took place in approximately equal quantities, regardless of species, or of different portions of any one species (see the notes on staminate flowers below). Fluctuations produced differences of less than 1° among foliage types, but, since signs frequently reversed, differences tended to cancel.

Rain

Rain at night had the same effect as it had in the daytime. Differences between air and trees were present, and of either sign, but were negligible.

The foregoing observations contain points of interest from the standpoint of insect ecology. The increased differences observed during the spring indicate that, while a sheltered thermograph might register a 24-hour temperature range of some 15 degrees, insects nearing the end of their period of hibernation upon the twigs of trees may be experiencing a range of 21 or 22°. Furthermore, 5° or more of this range lies at temperatures above the maximum shown by the thermograph. Under summer conditions, when insects are feeding on leaves, this difference is increased, as shown in the notes on summer temperature levels.

The observations on rolled and normal aspen leaves, which suggest the possibility of the importance of angle of incidence, raise a point which is not of direct entomological concern, but is nevertheless interesting. Many specimens of the black spruce (*Picea mariana* BSP.) exhibit typically pendulous branches. Bursting of the buds of this species occurs later than in other species of spruce. Doubtless this delay is largely a result of specific differences, but it would be interesting to examine the possibility of whether or not the angle at which buds are held in spring sunlight by the drooping branches is of importance to the observed discrepancy in phenology. The question might have some bearing on problems centred on the habits of the spruce budworm.

A Frontal Sequence

Figure 2 is a composite illustration showing changes in various meteorological factors over a four-day period in the latter half of August. The upper portion of the figure shows the changes in wind direction and atmospheric pressure associated with the approach and passage of a warm front, which, at the ground, passed over the station area about 0400 on the third day. Note that the wind at night commonly had a northerly component. This periodic variation complicated the picture slightly, but if it is taken into account while the record is examined, the shifts of wind direction associated with the front are clear. The temperature curves illustrated are based on half-hourly abstracts, in order to obtain an intelligible curve at a reduced scale. This method has the disadvantage that many of the independent fluctuations of the plant temperatures are lost.

The internal temperature of a developing cone of *Pinus Banksiana* (solid line) should be compared to the air temperature (dotted line) at the same level, 2m. The broken line shows the fluctuations of soil surface temperature, measured on sand near the base of the tree, and the remaining line shows the temperature of a grass blade 5 mm. above the soil surface point. It is particularly interesting to observe the effects of nocturnal radiation on the grass-blade temperature as compared to the soil surface temperature. The basis for dew formation on turf is clear.

On the first day of the series, broken cumulus occurred until 0900. Thereafter, scattered cumulus persisted until 1400, after which only isolated clouds occurred. By 1700, the sky was completely clear, but in the early evening, remnants of the day's clouds occasionally passed over.

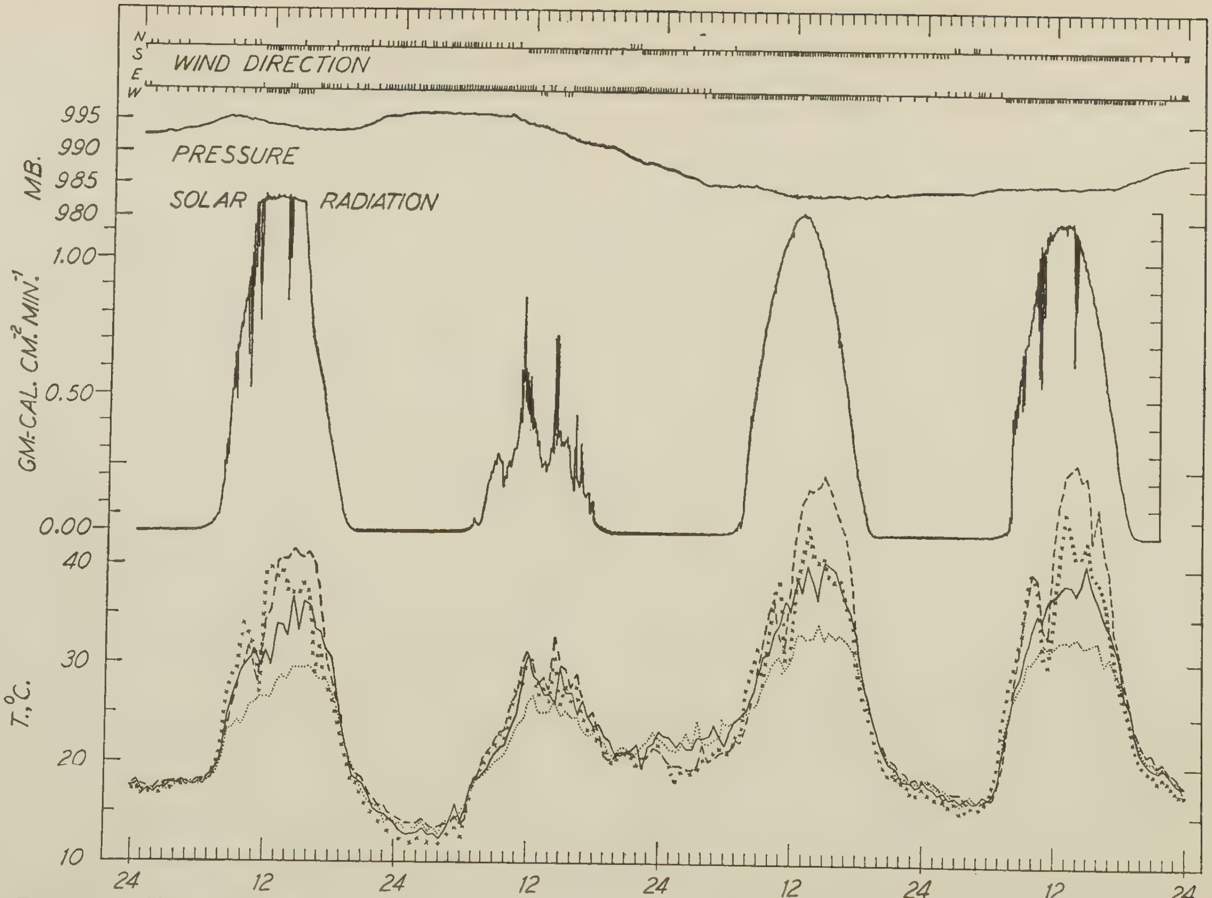

FIGURE 2. Changes in meteorological factors and associated variables over a 4-day period during which a warm front passed over the station on the third day. Abscissa: time, in hours. Ordinate (temperature curves): dotted line, air temperature at 2 m.; solid line, internal temperature of a developing cone of *Pinus Banksiana* at the same level; broken line, sand surface temperature at the base of the tree; crosses, grass blade temperature 5 mm. above the soil surface.

On the second day, an altostratus overcast appeared just after 0700, and, thereafter, the sky was clouded (4–10/10), with altostratus and altocumulus predominating. At 2000, there were 8/10 altocumulus, and the sky was occasionally completely overcast during the night, as also is shown by the temperature curves. Only a trace of rain was found in the gauge the next morning.

The third day was cloudless by 0800, and the sky remained so throughout the day and night, although there was a persistent, heavy haze. The fourth day was characterized by the appearance of a few fair weather cumulus clouds, but remained hazy and hot.

Special Situations

The preceding summation of differences observed between the temperatures of buds, shoots or leaf surfaces and that of the surrounding air showed that, particularly during the hours of daylight, large differences exist. In the present section, differences of particular entomological interest or those which have been observed in special situations are described.

Coniferous Staminate Flowers

The flowers of coniferous species exhibited internal temperatures which were considerably higher than ambient temperatures in direct spring sunlight. Figure 3 shows a series of records taken over a 24-hour period. One junction was inserted in a staminate flower of white spruce, another was inserted in a vegetative bud which had burst and was showing green foliage for a total length of 5 mm., while a third junction was installed nearby to measure air temperature. On the day in question, the area was occupied by a polar air mass which had moved over the region during the preceding 24 hours. Post-frontal heavy cumulus had broken during the preceding 12 hours and the air mass had been slightly modified. Nevertheless, air temperatures were still relatively low, despite the presence of a clear sky and bright sunlight. Winds were of the order of 8 to 18 m.p.h. (3.4–7.9 mps) during the day, dropping to 3 m.p.h. (1.5 mps) or less during the night.

The curves shown in the figure were plotted by taking the temperatures at 10-minute intervals and joining the points with straight lines. The method permits retention of the major fluctuations, and illustrates the major differences involved, together with any reversals of trends. The part of the figure illustrating the daylight period shows that the flower was 5 to 8.4° above the temperatures of the vegetative bud, and often ranged 10 to 14.5° above the air temperature. The slight displacement of the maximum of the flower curve into the morning stemmed from the fact that the flower cluster observed was orientated slightly east of south, whereas the vegetative bud was orientated almost due south. The crossing of the temperature curves for flower and bud about 1600 rather than later in the day also was a result of the orientation difference. The significant features shown are the wide discrepancies among the three curves and the length of time these differences were maintained. As a matter of general interest, this figure also shows the displacement of the air temperature

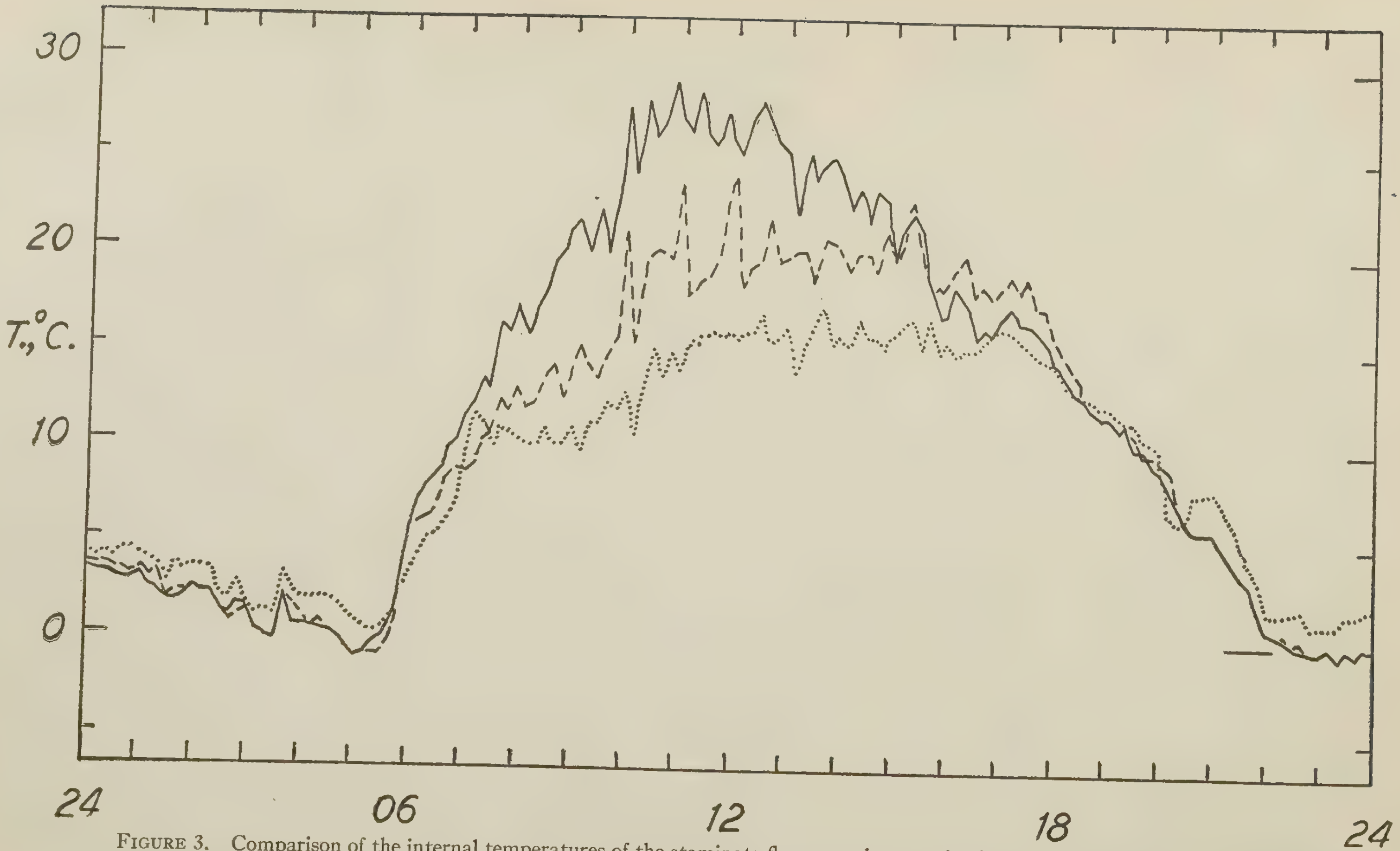

FIGURE 3. Comparison of the internal temperatures of the staminate flowers and vegetative buds of white spruce with the surrounding air temperature within a typical spring polar air mass. Abscissa: time, in hours. Ordinates: Dotted line, air temperature; solid line, flower temperature; broken line, vegetative bud temperature.

maximum towards the mid-afternoon, after some decline of solar radiation, and the maintenance of air temperature at a relatively steady value through the later afternoon, while the tree temperatures, dependent upon immediate insolation, continued to decline.

The immediate entomological significance of the foregoing illustration stems from current interest in the spruce budworm. During the spring, second stage larvae move from their hibernacula on the twigs to their feeding stations at or near the tips of branches. Larvae commonly feed among flowers when these are available. A glance at the accompanying figure shows that staminate flowers provide a much more efficient "greenhouse" when low air temperatures prevail than do vegetative buds. Thus, flowers provide conditions which would tend to accelerate the developmental rate during early instars by permitting steadier feeding. Since the first portion of the feeding stage is a critical period in the development of most lepidopterous larvae, interruptions then being reflected adversely in later stages, the superior "greenhouse" effect of staminate flowers may be of some importance.

During the period of the year when flowers are available to larvae, weather conditions in northern Ontario are characterized by frequent invasions of polar air masses similar to or colder than the one illustrated above. Laboratory tests of balsam staminate flowers indicated that they cooled more slowly than did buds or needles when a source of radiation was cut off, but curves obtained in the field under rapidly moving turbulence cumulus, the typical spring cloud type, showed no special evidence of any advantage gained from the slower cooling rate, because the clouds travelled too rapidly to deplete incoming radiation seriously. With broken, rather than scattered cloud, the slower rate of cooling might operate in favour of budworm larvae feeding in flowers, since it would maintain their environment above the prevailing low air temperatures which are often below 10° C. during cloud passages taking 10 or 12 minutes.

Figure 3 also shows that, for the most part, the flowers and the vegetative bud exhibited no difference in temperature during the night. When nocturnal differences did occur, they were, with two exceptions, in favour of the vegetative bud. This is a further indication that the flowers were closer approximations to a "black body" than was the bud. Nevertheless, differences at night, from the practical standpoint, lack the significance of the greater differences exhibited in sunlight, or the summer nocturnal differences exhibited between air and any foliage temperature.

In the field, balsam fir flowers were not observed under conditions so ideal as those which existed when spruce flowers were measured. A considerable amount of thin cloud occurred during the measuring period. Nevertheless, at air temperatures ranging between 10 and 20° C., daytime records showed flowers ranging 2 to 5.5° above vegetative buds, which, in turn, were 2 to 5° above the surrounding air. Jack pine flowers were inferior to white spruce flowers in sunlight, but they still ranged 2.7 to 5.5° above the bud temperatures.

Spruce Budworm Internal Temperature

Gunn (9) and Uvarov (23) have reviewed work on the effects of radiant heat upon insectan internal temperatures. Previous work under field conditions has, for the most part, been confined largely to investigations of the temperatures of locusts in relation to ambient temperatures. The results suggest that a common source of error in applying laboratory data showing the effects of temperature upon behaviour, development or survival of various insects, has resulted from neglect of radiation in the field. During the study of reactions of the larvae of the spruce budworm to light (26) it was found necessary to measure the body temperature of sixth stage larvae under natural conditions. This work was extended somewhat for the present purposes, and some of the data are included here, since they show that a lepidopterous form is affected similarly to locusts.

To measure the internal temperatures of a larva under field conditions, a thermojunction was inserted into the digestive tract through the anus so that the junction rested in the vicinity of the mid-gut. Table 2 gives sample hourly readings, expressed as differences from ambient temperatures, of two of a number of living larvae which were exposed to atmospheric conditions for 24 hours in late June.

TABLE 2.—INTERNAL TEMPERATURES, IN CENTIGRADE, OF TWO SIXTH STAGE LARVAE OF *Choristoneura fumiferana* (CLEM.) DURING A TWENTY-FOUR HOUR PERIOD

Time: EST.	Air temperature	Larval temperature — $\Delta L_1T - AT$	Air temperature $\Delta L_2T - AT$
0000	3.4	−0.1	−0.5
0100	2.0	0.1	−0.2
0200	1.7	−0.1	−0.5
0300	1.8	−0.5	−0.6
0400	1.7	0.0	0.0
0500	2.5	0.4	0.1
0600	6.9	0.2	0.0
0700	11.5	1.7	1.6
0800	16.5	1.5	2.7
0900	20.0	2.2	2.2
1000	21.6	2.9	1.8
1100	23.7	3.0	1.7
1200	28.2	0.5	−0.2
1300	29.6	−0.2	0.5
1400	27.5	−0.1	0.2
1500	26.4	0.7	0.5
1600	26.2	1.1	0.8
1700	28.2	0.1	−0.1
1800	25.7	0.5	0.9
1900	21.7	−0.2	−0.5
2000	16.0	−0.1	−0.3
2100	12.5	−0.5	−1.4
2200	10.0	−0.1	−0.4
2300	9.2	0.7	0.1
2400	9.0	−0.5	−0.2

The weather during the period was as follows: the preceding evening had been partly cloudy, and the cloud was dissipating near midnight. Scattered patches came overhead occasionally, and some of these occurred

at the hour points given (e.g., –0400). Thereafter, the sky was cloudless, but hazy, until after 0800. Scattered patches of altocumulus and cirrus appeared at 0900, and continued to move over the station throughout the rest of the period, which accounts for the lowered temperatures or the reversals of sign near midday and through the afternoon. Slight discrepancies between the two larvae were a combination of individual variation and differences in overlying shadow pattern. The most important point shown is that when the larvae were fully exposed to the atmosphere, their internal temperatures during sunlit periods were quite consistently above the surrounding air temperature, and during the brief periods of radiant cooling at night, fell slightly below ambient temperature. The highest elevation above air temperature during the day occurred at 1230, when the internal temperature of larva 1 was 3.9° above the air.

There may be some objection to the observations described above, on the grounds that sixth instar budworms normally feed in loosely-constructed shelters which they fashion by webbing together some of the needles of a shoot. One reason the above readings were taken in the manner described was that continuous records throughout a twenty-four hour period were required, and it was impossible to make such readings in a budworm tunnel for that length of time, since the silk allowed a larva sufficient traction to pull itself free of the junction after a short time. However, to meet any objection, some readings were taken for short intervals of larval internal temperatures within the natural tunnels. At the same time, the temperatures of the air enclosed in the tunnel and the outside air were recorded, together with the moisture contents. Readings were taken in early July, when somewhat higher temperatures than those previously noted were prevalent. Some of the pertinent records are listed in Table 3.

This table lists the internal temperatures, expressed as differences from air temperature, of some of the sixth stage larvae tested. During the observations, the sky remained cloudless, but there were occasional periods with light haze. Flecked shadow from overtopping foliage approached the observational point near the 1410 reading, and, thereafter, the flecked shadow slowly changed to an apparently continuous one. The differences listed are large and require little additional comment, but it should be noted that some of the negative values resulted from sudden upsurges in air temperature to points above the temperatures inside the tunnels. The wind remained close to 15 m.p.h., with gusts, and the upsurges resulted from sudden passages of warm currents.

Although the primary concern here is with the effects of radiation, it is of interest to note that the tabular data give some indication of the effects of atmospheric moisture upon the internal temperatures of the insects. Furthermore, with the exceptions of the tunnels of larvae 1 and 4, which were very loosely webbed, the humidities listed, when converted into units of evaporation (28), closely approximate the evaporation preference determined for exposed larvae of the same stage in earlier laboratory work (29).

TABLE 3.—INTERNAL TEMPERATURES, IN CENTIGRADE, OF SIXTH STAGE LARVAE OF *Choristoneura fumiferana* (CLEM.) CONCEALED IN FEEDING TUNNELS, TOGETHER WITH TEMPERATURES AND RELATIVE HUMIDITIES OF AIR INSIDE AND OUTSIDE THE TUNNELS

Larva No.	Time: EST.	Air temp.	Tunnel temp. – air temp.	Larval temp. – air temp.	Air R.H.	Tunnel R.H.
1	1143	29.3	0.2	1.0	54.0	96.0
	1145	30.6	−1.6	−0.7	49.0	89.0
	1147	26.7	1.0	2.1	60.0	83.5
	1151	25.8	0.7	2.3	64.0	78.0
	1153	28.0	0.5	1.7	52.0	78.0
	1156	27.0	2.0	3.8	58.0	77.0
	1200	28.5	1.5	3.1	54.5	83.0
	1202	28.1	1.4	2.5	53.0	82.5
	1205	30.6	−0.7	0.5	51.5	81.0
	1207	31.7	−4.7	0.4	43.5	96.0
2	1223	28.1	1.4	1.6	59.0	54.0
	1226	29.3	−0.8	0.6	48.0	61.0
	1230	28.8	0.7	2.0	57.0	60.5
	1233	29.0	0.3	0.7	49.0	53.5
	1236	29.7	0.0	0.6	45.0	59.0
	1238	27.1	1.9	3.2	63.0	56.0
	1241	28.1	1.2	2.5	57.5	57.0
	1244	28.0	0.1	2.3	53.0	63.5
	1246	25.8	2.3	3.7	64.0	57.5
3	1302	29.5	0.2	3.4	49.5	89.0
	1304	28.8	2.7	6.3	54.0	74.0
	1306	27.7	2.2	4.3	57.0	72.0
	1309	28.1	2.5	3.6	54.0	76.5
	1313	27.5	2.2	4.4	56.0	77.0
	1315	30.3	0.9	2.8	47.0	86.0
	1323	28.1	4.3	7.2	73.0	76.0
	1328	30.3	0.9	3.4	50.0	72.0
	1335	28.1	4.6	8.9	60.0	70.0
	1337	30.5	−1.0	2.9	49.0	76.0
4	1347	28.8	2.3	0.7	52.0	65.0
	1350	29.5	1.0	0.4	64.0	88.0
	1353	26.9	2.1	2.4	58.0	61.5
	1355	27.0	1.1	1.8	57.0	67.0
	1400	27.7	0.4	1.1	53.0	67.0
	1403	29.3	−0.3	0.0	48.0	63.0
	1407	25.9	2.2	2.9	67.0	61.0
	1410	25.9	1.2	1.8	59.0	57.5
	1413	27.7	−0.2	0.4	48.0	68.0
	1415	26.4	0.0	0.6	50.5	66.0
5	1433	30.5	−2.4	−2.5	56.0	91.0
	1438	29.3	−0.8	−1.2	55.0	88.0
	1442	28.8	−0.8	−0.7	71.0	89.0
	1445	27.0	−0.1	1.0	73.0	89.0
	1448	27.0	0.1	1.0	67.0	79.0
	1450	29.3	−0.5	−1.3	53.0	70.0
6	1457	29.5	−1.5	−3.6	57.0	75.0
	1500	28.1	−1.6	−1.4	68.0	85.0
	1502	29.7	−1.7	−3.2	64.0	75.0
	1506	28.1	0.9	−0.1	76.0	77.5
	1510	30.3	−0.6	−1.8	71.0	79.0
	1513	30.3	−1.3	−1.8	64.0	77.5
	1517	29.5	0.0	−0.7	66.5	65.0
	1521	29.5	−1.0	0.0	65.0	68.0
	1524	31.8	−1.9	−2.3	55.0	76.0
	1527	32.2	−1.7	−2.3	53.0	73.0

Temperatures in Large Tents and Webs

During 1949, preliminary investigations of the effects of physical factors on the behaviour and activity of three species of tent caterpillars (*Malacosoma*) and of the spotless fall webworm, *Hyphantria textor* Harr., were begun. The equipment and techniques described in the present paper have been used in the general investigative routine. Although the main body of data being accumulated forms a separate subject which will be reported elsewhere, some of the routine measurements of temperatures taken in the silken tents are pertinent to the present work. Table 4 contains representative readings taken in and upon a tent formed by a colony of *M. pluviale* (Dyar) in early June.

TABLE 4.—TEMPERATURES, IN CENTIGRADE, UPON AND WITHIN A COLONIAL TENT OF THE WESTERN TENT CATERPILLAR, *Malacosoma pluviale* (DYAR)

Time: EST.	Air temperature	Tent surface temperature	Tent centre temperature
0800	12.6	13.6	17.5
0830	15.0	18.8	29.5
0900	15.2	15.7	23.6
0930	17.6	21.5	32.3
1000	18.8	23.5	35.6
1030	20.6	21.5	34.5
1100	24.2	24.7	35.5
1130	24.0	23.7	33.5
1200	23.7	24.7	36.0
1230	22.2	23.2	32.0
1300	22.0	26.0	32.7
1330	24.6	25.2	33.2
1400	23.3	23.2	34.0
1430	25.3	26.3	33.7
1500	25.6	30.5	39.7
1530	25.0	28.0	40.0
1600	22.5	24.3	33.5

The tabular values are representative of the differences which may be observed under a broken sky containing cirriform clouds and a few altocumulus clouds. The effects of these may be seen near the midday readings, especially.

Temperature readings taken within the webs of colonies of *Hyphantria* in early August show very similar values. Web temperatures in full sunlight range 8 to 13° above the air temperature measured at the same level, with values around 40° C. for an air temperature of 25-27° C. On clear nights, the webs are about 1° cooler than the air.

Studies of behaviour still in progress indicate that larval movements from tents or within them are governed to some extent by the fluctuations of physical factors within the tents.

DISCUSSION

It is clear from the foregoing descriptions that solar and nocturnal radiation exert decided effects upon the immediate habitats of insects which feed upon or within the parts of plants. Also, it is clear that the magnitude of the temperature differences observed is such that neglect of their

existence may result in serious errors in attempts to relate laboratory and field results. Hitherto, entomologists appear to have recognized among such differences only those between air temperature and such values as subcortical temperatures of felled trees. To bark and cambial temperatures should be added those of buds, leaves, cones, flowers and, indeed, of the insects themselves. It has long been recognized that ordinary screen temperatures at times bear little relation to areas of entomological interest. However, the field situation is clearly very complex, and anyone wishing to obtain truly useful records must be prepared to work with something more than a mercury-in-glass thermometer. Blind acceptance of air temperature is a dangerous procedure, even when records are taken at a point of special interest. More attention should be paid to the behaviour of insects in their particular niches, and some effort must be made to analyse this behaviour in terms of changes in physical conditions, most of which (including evaporation) will be affected by radiation. Only when a good understanding of the behaviour mechanisms of a particular species has been reached can the relative importance of such factors as air temperature be correctly assessed.

It is worth re-emphasizing that, during initial tests to compare different types of instruments or different types of vegetation, comparable exposures are essential. This holds true not only in the vertical and horizontal planes at the periphery of any vegetation, but also in the space from the periphery to the interior of a tree. One finds a change in foliage climate a short distance inward from the periphery, particularly in a coniferous species. A brief inspection of the situation will show that the physical gradients inward toward a tree trunk are, in miniature, replicas of the more intense vertical gradients in the atmosphere from the forest floor to the canopy, the foliage in both situations acting to modify patterns of evaporation, convection and radiation, and, hence, of temperature. Some data on these points were accumulated in the present work, but the general situation in the forest is set forth so well in an earlier work (7) that repetition is needless.

SUMMARY

1. The observed differences between insect temperatures and the temperatures of the parts of plants on which they feed, on the one hand, and the temperature of the surrounding air, on the other, are sufficiently large to be given serious consideration in field studies.

2. The differences observed are largely a result of radiant heating by day and radiant cooling by night.

3. Under winter conditions, when the sun is at low elevations, heating is still sufficient to raise exposed coniferous foliage more than 2 Centigrade degrees above the surrounding air at latitude 46° 30′ North. By night, exposed foliage radiates down as much as 0.8° below the air temperature under a clear sky.

4. Snow-covered foliage remains above the air temperature on clear, calm nights, and below it during sunny days. This damping of daily fluctuations means that insects overwintering on branches beneath snow cover may experience about 8° less total change per day than insects on exposed branches.

5. Summer conditions give results somewhat similar to those observed during the winter, but values differ in degree. More intense incoming radiation by day raises vegetative parts as much as 8° above surrounding air, and more rapid rates of outgoing radiation at higher night temperature levels lower vegetation temperatures as much as 3° below the surroundings under a clear sky.

6. Wind does not modify temperatures elevated by radiant heating to a very marked degree, but it affects radiant cooling at night, particularly in winter when the decreased rate of cooling at generally low temperature levels is below that prevalent under summer conditions.

7. Winter cloud by day keeps exposed foliage slightly above air temperature, and by night re-emitted radiation from low cloud raises foliage temperatures fractionally above the air. Summer cloud by day permits elevation of foliage temperatures to 2° above the air. At night, an overcast seldom maintains foliage temperatures a significant amount above the surrounding air.

8. When isolated clouds obscure the sun, but not the rest of the sky, at any season, foliage radiates to levels below air temperature. Similarly, foliage exposed to the sky, but shielded from the sun, cools by radiation. If broken cloud is present, diffuse radiation keeps such foliage from cooling.

9. Spruce budworm larvae in their natural webs experience temperatures up to 8° above ambient conditions in midsummer.

10. Different parts of trees differ in their capacities to respond to radiant heating. Staminate flowers of coniferous trees commonly are at temperatures 5° to 8° above vegetative buds in sunlight. Since the buds, in turn, are above air temperature, this is an important difference for insects with habits like those of the spruce budworm.

11. The silken tents constructed by colonial species trap air which frequently ranges 8° to 13° above outside air in full sunlight.

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